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THE RODENTS OF THE DESEADAN OLIGOCENE OF PATAGONIA AND THE BEGINNINGS OF SOUTH AMERICAN RODENT EVOLUTION

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INTRODUCTION

Several years ago, one of us (Wood, 1949) undertook the study of two excellent rodent skeletons from the Deseadan of Patagonia in the collections of The American Museum of Natural History. This work emphasized the need for a review of the Deseadan rodent fauna as a whole, a project that we had had in mind for many years and for which each of us had been taking notes in somewhat desultory fashion. A first draft, based on material in the Amherst collection, was written by Wood. This was revised and extended by Patterson on the basis of specimens in Chicago Natural History Museum, The American Museum of Natural History, and the Muséum National d'Histoire Naturelle. A second draft, on which we collaborated, was then prepared. After this had been completed, the opportunity to convert the review into a monograph was afforded by the award of a John Simon Guggenheim Memorial Foundation Fellowship to Patterson for work in Argentina. Study of the types and other specimens in the Ameghino Collection revealed so much that was interesting and unexpected that the second draft had to be extensively revised. We then collaborated on the writing of a third draft. This was finally rewritten to include a discussion of the series of important papers on rodent phylogeny that have appeared during the last eight years. The work has indeed been a long time in preparation, but we believe that its present completeness fully justifies the delay.

The number of specimens available is surprisingly large. There are approximately 70 (mainly isolated teeth) in the Muséum

National d'Histoire Naturelle; 54 (including many complete jaws or upper dentitions) in the Amherst College Museum; 27 in the Ameghino Collection, now preserved in the Museo Argentino de Ciencias Naturales; 9 in Chicago Natural History Museum; 9 in the Yale Peabody Museum; 5 in the Museum of Comparative Zoology; and 11 in The American Museum of Natural History; a total of over 185. Loomis (1914, p. 20) mentions 102 rodent specimens, all but 6 being *Cephalomys,* collected by the Amherst Expedition (not by the Princeton Expeditions, as stated by Landry, 1957a, p. 53 — the Princeton Expeditions, to Hatcher's sorrow, never saw the Deseado). In his text, however, (pp. 189, 190 and 192) Loomis gives totals of specimens under individual species of *Cephalomys* that add up to 79, for a total rodent collection of 85. We have found 74 numbered specimens collected by Loomis (54 in Amherst, 9 in the Yale Peabody Museum, 5 in the Museum of Comparative Zoology and 6 in the American Museum of Natural History). Some of these consist of groups of isolated teeth. We do not know whether this is Loomis' entire collection, or whether there are, in other museums, additional specimens, or lots, that we have not been able to locate.

The locality known as Cabeza Blanca on the Río Chico del Chubut, Province of Chubut, has yielded the largest number of specimens. All of the specimens in Amherst, Yale and the Museum of Comparative Zoology, all but two of the Chicago specimens, and all but three of the American Museum specimens are from here. To judge from the color, preservation, adhering matrix and one of two labels preserved with them,[1] all but one

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[1] This label reads "Gran yacimiento del Pyroterio-Río Chico," which can only mean Cabeza Blanca. Other labels clearly referring to this locality read "1er yacim. Pyroth. Río Chico," i.e. the first Deseadan (*Pyrotherium* beds) locality encountered on the way up the valley of the Río Chico del Chubut. It might be assumed from the wording that this was *the* first Deseadan locality found by Carlos Ameghino, but such is not the case. Isolated remains of Deseadan mammals from Neuquen (*Pyrotherium romeri, Trachytherus spegazzinianus, Parastrapotherium ephebicum*) reached Florentino Ameghino during 1885-1889, and Carlos had come across Deseadan localities in Santa Cruz and Chubut during 1888-1892, but was prevented by unfavorable circumstances from making collections. It was not until his seventh expedition to Patagonia, 1893-4, that Carlos was able to collect a Deseadan fauna and to prove that the beds lay beneath the Patagonian formation. The material collected during this expedition formed the basis of Florentino's first paper on this fauna, his "Première Contribution" (Ameghino, 1895, pp. 603-606). Judging from the forms represented, the color and preservation of the specimens, the adhering matrix and such labels as are present, there can be no doubt that the locality or area was that now known as La Flecha in Santa Cruz Province, situated a little distance to the south of the inlet of the Río Deseado. This, then, should be considered the type locality. By a happy coincidence, most of the Deseadan material, collected by Tournouër and studied by Gaudry, who proposed the name Deseado, came from this locality. The localities at Cabeza Blanca and Lake Colhué-Huapí were not discovered by Carlos Ameghino until 1894-1896, and material from them was first described by Florentino Ameghino in his "Deuxième Contribution" (1897c).

of Ameghino's specimens are also from this locality. The *Platypittamys* material in the American Museum is from the Scarritt Pocket, Rinconada de los Lopez, Chubut. All of the material in the Muséum National d'Histoire Naturelle is from La Flecha, Santa Cruz, as are the specimens not from Cabeza Blanca in Chicago Natural History Museum and in the Ameghino Collection. The specimens in the Ameghino Collection were, of course, collected by Carlos Ameghino; those in the Muséum National d'Histoire Naturelle by André Tournouër; those obtained by the Amherst College expedition were collected by Frederick B. Loomis, William Stein, Waldo H. Shumway and Phillip L. Turner; in Chicago Natural History Museum by Elmer S. Riggs, John B. Abbott and George F. Sternberg; and those from the Scarritt Expedition, in The American Museum of Natural History, by George Gaylord Simpson, Coleman S. Williams and Justino Hernandez. Tournouër was the only collector who found rodents in numbers at La Flecha. He very probably happened upon a small pocket containing them. The fact that Carlos Ameghino, who clearly had a magnificent eye for minute specimens, found only one isolated molar there is sufficient proof that they are really rare at the locality. The Chicago specimens from there consist of a ramus, and of an isolated molar that was found, during preparation, in the matrix surrounding a large mammal.

To date, seven genera have been described from the Deseadan: *Cephalomys, Asteromys* and *Orchiomys* Ameghino 1897, *Eosteiromys* Ameghino 1903, *Scotamys* and *Litodontomys* Loomis 1914, and *Platypittamys* Wood 1949. The Deseadan species *medianus*, referred by Ameghino to *Eosteiromys* (type species *E. homogenidens* Ameghino 1902 from the Colhué-Huapí) is here made the type of a distinct genus, *Protosteiromys*, and two other new genera, *Deseadomys* and *Chubutomys,* are proposed. *Orchiomys* is shown to be a synonym of *Cephalomys.* Eight genera and twelve species of Deseadan rodents are now known, but fragmentary remains too incomplete for formal description show that we are as yet far from a complete knowledge of the fauna. The phylogenetic relationships are very interesting and, for the most part, quite determinable. Six families, representing all four of the currently recognized superfamilies of South American rodents, are represented. Despite this apparent diversity, the Deseadan is not far from showing the basic stage from which the indigenous Neotropical rodent fauna has been derived.

Each of the adequately known forms has been compared with its possible ultimate ancestors, particularly the North American Paramyidae and Sciuravidae, the European Theridomyidae, and the African forms included by Wood (1955, p. 172) in the Phiomyidae, although these comparisons may not always be discussed in detail. In no case does the material here considered warrant the statement that any known form from the rest of the world is definitely ancestral to the Deseadan rodents. It is possible, however, to arrive at what we consider to be reasonable inferences as to the source of the South American rodents, and we have gone into this matter at length after the description of the fossils.

In addition to the Guggenheim Foundation Fellowship, this study has been assisted by grants to Wood from the Marsh Fund of the National Academy of Sciences, by tenure of a Cutting Traveling Fellowship from Columbia University by Wood, which afforded the opportunity for first hand study of numerous theridomyids, by tenure of a Carnegie Corporation Grant-in-aid for Travel awarded to Patterson by the American Association of Museums, which made possible a preliminary examination of the Deseadan material in the Muséum National d'Histoire Naturelle, and by a grant from the National Science Foundation to Wood, which permitted, incidental to other work, the statistical analysis of the material belonging to *Cephalomys*. We wish to express our sincere thanks to Professor Camille Arambourg, Muséum National d'Histoire Naturelle; Dr. George Gaylord Simpson, The American Museum of Natural History; Dr. J. T. Gregory, Yale Peabody Museum; and Drs. Agustín E. Riggi, Noemí Cattoi and Jorge L. Kraglievich, Museo Argentino de Ciencias Naturales, for their kindness in permitting the study and description of material in their charge. We are especially obliged to Professor Arambourg for sending the Tournouër Collection to us for detailed study. The statistical studies were made by Frances W. Wood, for whose assistance in this and in many other ways we are deeply appreciative. Regression lines were calculated by Mr. Craig C. Black. The aid of Mrs. William D. Turnbull and of Mrs. Elizabeth E. Wareham in preparing several

drafts of the manuscript is gratefully acknowledged. Figures 21, 24 and 26 were drawn by Señorita Estela Lescano, Figure 1 by Mrs. Dorothy Marsh; the remainder are by Wood.

The following abbreviations are employed: A.C.M., Amherst College Museum; A.M.N.H., The American Museum of Natural History; C.N.H.M., Chicago Natural History Museum; M.A.C.N., Museo Argentino de Ciencias Naturales; M.C.Z., Museum of Comparative Zoology: M.N.H.N., Muséum National d'Histoire Naturelle; and Y.P.M., Yale Peabody Museum.

MOLAR TERMINOLOGY AND MEASUREMENT

As discussed in detail on later pages, we believe that all indigenous South American rodents were derived from ancestors whose molars had four transverse crests on each tooth, both uppers and lowers. Adopting the terminology suggested by Wood and Wilson (1936), we employ the following terms for these crests: anteroloph, protoloph, metaloph and posteroloph in the upper teeth; anterolophid, metalophid, hypolophid and posterolophid in the lowers (Fig. 1). There is some uncertainty, due to a tendency to shift position, as to whether the terms protoloph and metaloph in the upper teeth, and metalophid and hypolophid in the lowers, are strictly applicable throughout, or whether such terms as protolophule II or hypolophulid I should be employed in some cases. The crests are strictly homologous throughout this group of rodents, however, and we have therefore thought it best to employ a uniform nomenclature rather than to introduce new terms whenever shifts occur in the relation of, say, the protoloph to the protocone or of the hypolophid to the hypoconid.

For the valleys between these crests, we have borrowed terms from Stirton's nomenclature for castorid teeth (1935), as modified by Black and Wood (1956). In the uppers, these are: paraflexus, mesoflexus and metaflexus (external) and hypoflexus (internal); in the lowers: hypoflexid (external) and anteroflexid, mesoflexid and metaflexid (internal). Whenever a valley is converted into a lake, either by wear or by the complete union before wear of the extremities of the flanking crests, the endings -flexus and -flexid become -fossette and -fossettid, e.g. parafossette, metafossettid (Fig. 1). In general, our terminology agrees with that of Fields (1957, Fig. 2). We do not, however, agree with his use of parafossettid and paraflexid in the lower teeth since we cannot accept the implied suggestion that these teeth incorporate a paraconid, and we therefore prefer the terms anterofossettid and anteroflexid. A second point of disagreement concerns the ter-

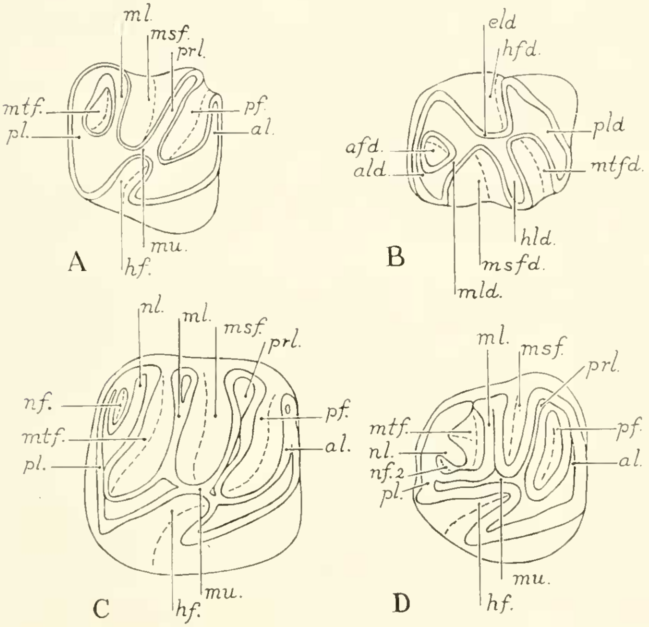

Fig. 1. Key to terminology applied to crests and valleys of molar teeth. *A* and *B*, RM^1 and RM$_1$ of *Deseadomys arambourgi* gen. et sp. nov.; *A*, A.C.M. no. 3163; *B*, type, M.N.H.N. no. 1903-3-1. *C*, LM^1, reversed, of *Protosteiromys medianus* (Ameghino), A.C.M. no. 3014. *D*, RM^3 of *Erethizon dorsatum epixanthum* Brandt, M.C.Z. no. 36718. *A-C*, x 6; *D*, x 3.

Abbreviations: *afd.*, anterofossettid; *al.*, anteroloph; *ald.*, anterolophid; *eld.*, ectolophid; *hf.*, hypoflexus; *hfd.*, hypoflexid; *hld.*, hypolophid; *ml.*, metaloph; *mld.*, metalophid; *msf.*, mesoflexus; *msfd.*, mesoflexid; *mtf.*, metaflexus or metafossette; *mtfd.*, metaflexid; *mu.*, mure; *nf.*, neofossette; *nf.2*, lingual neofossette; *nl.*, neoloph; *pf.*, paraflexus; *pl.*, posteroloph; *pld.*, posterolophid; *prl.*, protoloph.

minology in the lingual side of the upper teeth, where Fields calls the valley that separates the anteroloph from the protocone the hypoflexus, instead of using that term, as did Stirton and as do we, for the valley between the protocone and the hypocone.

There is a rather common tendency among South American rodents for the development of a fifth crest in the upper molars. Less commonly, a fifth crest may arise in the lower molars. These crests arise from the posteroloph above and from the anterolophid below. As pointed out farther on (pp. 334-336), they have nothing to do with the mesoloph and mesolophid of the Theridomyidae and other rodents; such crests do not occur in the permanent molars of caviomorphs. For descriptive convenience, we employ the terms neoloph and neolophid for these fifth crests, and neofossette and neofossettid for the lakes isolated by them. Fields' entoflexus and entofossette are the same as our neoflexus and neofossette.

We prefer definite names for these crests and valleys to such more general terms as first, second, etc. anticlinals and synclinals employed by Stehlin. The latter have the merit of simplicity but the defect of implying homology wherever used. A five-crested caviomorph molar and a five-crested theridomyid molar, for example, do not, we believe, have all their crests and valleys homologous.

The molar terminology is applied to structures on premolars that occupy the same position, relative to the tooth as a whole, as those on molars. It is recognized, however, that some of them, at least, may have had a different history. At the present time, the evolutionary sequence in rodent premolar development is often clouded. The development of the premolars in the Caviomorpha is a case in point.

The tooth measurements given are the maximum diameters, in millimeters, of the various areas measured. Depending on the nature of the specimen, they may be either diameter of the wear surface, maximum diameter of the extra-alveolar portions of the teeth, or the maximum diameter whether extra-alveolar or intra-alveolar. The second group of these measurements has been marked † and the last *. The diameters given are averages of two to four measurements. There is considerable variation in some of the high-crowned teeth as to the location of the maximum diameter. The measurements made from figures will not necessarily agree with those listed. The drawings have been made looking down perpendicularly on the wear surface. In many specimens, however, the wear surface is oblique to the long axis of the tooth, so that the drawing will show, for example, a considerable expanse of the lower part of the tooth on the lingual side of the crown, without indicating that there is an extensive overhang on the buccal side.

TAXONOMY AND MORPHOLOGY

Suborder CAVIOMORPHA Wood and Patterson 1955 (*in* Wood, 1955)

The Caviomorpha may be defined as follows: rodents with enlarged infraorbital foramen, through which progressively passes M. masseter medialis, pars anticus; infraorbital foramen frequently approaching orbit in size; angle of jaw of hystricognath type; malleus and incus fused or separate; dental enamel of multiserial type but derivable from an ancestral stock with enamel of pauciserial type; cheek teeth derived from an ancestral stock with four transverse crests on both upper and lower molars; permanent molars without mesoloph or mesolophid; metaloph and metalophid frequently unstable, disappearing in some groups; neoloph and neolophid arising in some groups from posteroloph and anterolophid respectively; restricted to the New World. Known distribution: Oligocene to Recent, South America; Pleistocene to Recent, North and Central America and Antilles.

In addition to these characteristics, several supplementary myological features may be cited. M. palmaris longus generally arises from the olecranon or is lost, though in the erethizontids and caviids it arises in the primitive manner from the medial epicondyle, as it does in the Old World hystricomorphs. M. trapezius is generally divided into two or three separate elements, although it is a continuous sheet in the erethizontids, as in *Aplodontia* and *Hystrix;* in the African *Petromus* there are three elements. M. omohyoideus is progressively lost, whereas it is present in the Old World Hystricomorpha. M. sternoscapularis is present in its entirety, but the fibers of the two halves are separated at the clavicle, as in *Petromus,* whereas they are continuous in *Hystrix* and *Thryonomys.* There is a tendency to lose the inner head of M. brachialis. The insertion of M. pronator teres has shifted from the distal to the proximal part of the radius.

Perhaps these muscle variants are of no great importance in themselves, but it appears to us that they are as significant in separating the Caviomorpha from the Old World Hystricomorpha as are myological characters sometimes cited as favoring the union of the two groups. Of all the characteristics that have been used to classify rodents, there are none so subjective as variations in muscles, no two authors ever seeming to give the same description for a given group of muscles. There are also few systems in the order where individual variation is less well understood.

Some caviomorphs possess five-crested molars, but the fifth crest (neoloph, neolophid), which was evidently acquired after the group had reached South America, is not homologous with the mesoloph or mesolophid of the Theridomyidae nor (probably) of the Hystricomorpha. In dm_4, of certain echimyids (*Protacaremys, Prospaniomys*) and erethizontids (*Erethizon* and *Coendou*) and in P_4 of some Santacruzian octodontids (*Sciamys*), a short crest may develop from the ectolophid posterior to the metalophid. Topographically, this occupies the position of the mesolophid in theridomyids and other rodents, but it is certainly an independent acquisition and does not extend posteriorly to the molar series. Within *Sciamys,* there is evidence that this and other minor crests posterior to the anterolophid developed essentially at random in P_4 (Patterson and Kraglievich, ms.).

On the basis of serology, Moody and Doninger (1956) conclude that there is no indication of special affinity between the Hystricomorpha and the Caviomorpha, based on studies of *Hystrix, Erethizon, Cavia* and *Dasyprocta.* Still another line of evidence that may be cited is that of ectoparasites, Vanzolini and Guimarães (1955 a and b) pointing out that there is no special relationship between the lice of caviomorphs and of hystricomorphs.

We believe that the indicated relationships warrant the separation of the South American rodents as a distinct suborder, the Caviomorpha. We believe that it can be considered as demonstrated that the South American forms were not descended from the European Theridomyidae, whether or not any of the Old World forms were. There does not seem to be any possibility that the Old and New World rodents generally placed in the "Hystricomorpha" (*sensu lato*) could have had a common ancestor later than the Early Eocene members of the Paramyidae. The similarities between the Old and New World forms must then all be examples of parallelism. Cabrera (1927) has reached broadly comparable conclusions, although without presenting supporting evidence. Lavocat (1951b) expressed a similar opinion, although he continued to place the Old and New World forms in a common group, based on jaw structure, and distinct from that in which the Paramyidae are placed. In another paper (1951a), he questioned there being any special relationship between the two groups, although later (1956), as discussed below, he returned to the possibility of special, though not close, relationships. Schaub (1953 a and b), Viret (1955), and Landry (1957a) have supported affinity between the Old and New World "hystricomorphs," which we do not accept for a variety of reasons given in detail below.

Since there are morphologic grounds on which the Old and New World "hystricomorphs" can be separated from each other, and since the paleontologic and particularly the paleogeographic evidence is against the two groups having a common ancestor later than the Early Eocene, we feel entirely justified in establishing a suborder for the South American forms, even though the morphologic criteria for doing so may appear to be neither exceptionally strong nor exclusive to the group. Similar situations will almost certainly be encountered as knowledge of rodent phylogeny improves. The classic subordinal divisions do not, it seems to us, stand on a secure foundation, and, in view of the abundantly demonstrated prevalence of parallelism in the order, can hardly be expected to stand unmodified indefinitely.

The microstructure of the dental enamel provides an interesting case in point, and one with a direct bearing on the present question. Over a hundred years ago, in his classic work on the microstructure of rodent enamel, Tomes (1850) showed that the crossing enamel layers in the incisors of "hystricomorphs" were each composed of several laminae of enamel prisms, a character that set them apart from other rodents. Here, seemingly, was a character as fundamental as the zygomasseteric structure for uniting Old World and New World "hystricomorphs" in the same suborder. Korvenkontio's magnificent work on the same subject (1934) suggests another interpretation, however. The "hystricomorphs" are indeed characterized, as Tomes showed, by crossing enamel layers composed of several laminae, Korvenkontio's multiserial type, in contrast to "sciuromorphs" and "myomorphs," which have the crossing layers composed of a single lamina, the uniserial type. Korvenkontio shows, however, that early, very primitive rodents have a type of enamel structure, which he calls the pauciserial type, that is intermediate between the two extremes, having neither as many laminae to a layer as in the multiserial nor as few as in the uniserial. The pauciserial type occurs both in paramyids and in some theridomyids.[2] It seems clear to us, therefore, that enamel of multiserial type could have been evolved independently by the ancestors of both the Hystricomorpha (*sensu stricto*) and the Caviomorpha; the evidence from the histology of the teeth does not now conflict with other evidence derived from gross morphology and from distribution. Sections of an isolated incisor from the Deseadan, probably of *Scotamys*, have been prepared. These show that, as might have been anticipated, multiserial enamel had already been acquired by this time.

The relations of the malleus and incus provide a similar case. Doran (1878, p. 418) stated that in the "Hystricomorpha" these ossicles were almost invariably fused in adults. Tullberg (1899, p. 69) gave such fusion as a character of his Hystricognathi, and Landry has recently (1957a, p. 16) given it great prominence as an item of evidence in favor of the unity of the Hystricomorpha (*sensu lato*). It must be noted, however, that Cockerell and Miller (*in* Cockerell, Miller and Printz, 1914, p. 372) found these ossicles to be separable in *Proechimys*.[3] We find that in *Echimys armatus*,

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[2] Because some theridomyids have the pauciserial type of enamel and some have the uniserial type, Landry (1957a, pp. 27-28) following Korvenkontio, considers that the Theridomyidae are a composite group, with members belonging to two suborders. This appears to us to be a misinterpretation of the data, which merely indicate that, in this feature, the Theridomyidae are in process of passing from a pauciserial to a multiserial type. The discovery of such transitional forms should, of course, come as no surprise.

[3] These authors also questioned one of Doran's exceptions, a young specimen referred by him to *Octodon*, stating that this looked very sciurine to them. They were quite right; a malleus and an incus of *O. degus* extracted by us from a skull are typically caviomorph in structure and bear no close resemblance to the bones so labeled by Doran.

Octodon degus, Spalacopus poeppigii and *Aconaemys* sp. the malleus and incus are not fused. Since the Octodontidae and Echimyidae are the most generalized of the caviomorph families, we strongly suspect that the lack of fusion in their auditory ossicles indicates that such fusion was acquired independently within the Caviomorpha.[4] The condition of the malleus and incus of *Pedetes* is of some interest in this connection, as showing that very close union is not confined to caviomorphs and hystricomorphs. Landry, following Tullberg, states that in this form the ossicles are separate, and that "this character, therefore, has proved useful in separating dubious groups from the Hystricomorpha" (*op. cit.*, p. 16). Doran had stated that these ossicles were fused in *Pedetes.* Upon investigation we have found them to be separable but with opposing surfaces complexly interlocking in both the vertical and horizontal planes. There is clearly even less possibility of movement between the two bones than in octodontids and echimyids. This anomalous rodent thus exhibits a "sciurognath" mandible, a "hystricomorph" zygomasseteric region, "hystricomorph" enamel, a "sciurognath" pterygoid fossa, and a malleus and incus at least as "hystricomorph" in degree of union as are some of those occurring in caviomorphs. *Pedetes* is, in fact, a standing warning against too dogmatic statements as to what does and what does not characterize major groups of rodents.

Our suborder Caviomorpha is not a new concept. The word "caviomorphs" was used by Simpson (1950, p. 376) for exactly the same group that we are including in the Caviomorpha, but without being formally proposed as a subordinal term, and without definition. Lavocat (1951b, p. 72) proposed a number of divisions of the rodents including one, the "Orthohystricognathes," for the forms we include in the Caviomorpha. Schaub (1953a) established an Infraorder Nototrogomorpha for the same group. Wood (1955, p. 180) proposed the suborder Caviomorpha, crediting it to the present authors. For reasons which we elaborate below, we feel that both Lavocat's and Schaub's

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[4] As Fields (1957, p. 347) implies, the auditory ossicles of rodents merit more study than they have received. As a minuscule contribution to this subject, we may record the following additional data as to fusion : *Abrocoma cinereus,* juv., separable ; *Abrocoma bennetti murrayi,* adult, inseparable ; *Ctenomys magellanicus,* adult, inseparable ; *Thryonomys swinderianus angolae,* juv., inseparable, area of fusion involving part of crus longus of incus.

terms contain phylogenetic implications that we distrust, and we are therefore continuing to use Caviomorpha, which, we feel, carries the minimum of phylogenetic implications involving other groups. The rules of priority do not apply to subordinal units, but it is possible to make a legalistic (although not very impressive) argument, if one wanted, that Simpson's usage establishes the priority and that neither Lavocat nor Schaub provided diagnoses or definitions. In any event, we feel that the entire problem of the subordinal and superfamilial arrangement of the rodents is at present in a state of flux, and that the next decade will see a considerable alteration in our knowledge of rodent relationships as indicated by subordinal terminology, so that the precise terminology now employed makes little difference.

Superfamily OCTODONTOIDEA Simpson 1945
Family OCTODONTIDAE Waterhouse 1839

Acaremyinae Ameghino 1902
Acaremyidae Wood 1949

The most surprising result of a revision of the *Acaremys-Sciamys* group and a comparison of these forms with Pliocene and Recent octodontids (Patterson and Kraglievich, ms.) was the realization that the former could not be separated from the latter, either as a family or as a subfamily. Winge (1924, pp. 73, 78) would appear to have been right in his reference of "*Acaromys*" and "*Sciomys*" to his Octodontini, Octodontes. A gap exists in our knowledge of the Octodontidae between the Santacruzian and the Huayquerian, but *Sciamys* on one side of this gap and the Pliocene forms on the other are sufficiently close to each other in dental and cranial characters as to permit no doubt on this score. *Sciamys* has rooted molars but, in contrast to those of the contemporary *Acaremys*, these were well on the way toward attaining the hypsodont condition. This trend was carried to completion, and cement added, during the hiatus in the history of the family. The later forms are nearly all hypselodont, but the Huayquerian to Hermosan *Phtoramys* does develop roots in old age, and the changes in crown pattern that it displays are very similar to those seen in *Sciamys* and, more fleetingly, in *Acaremys*. The postcranial skeleton of the Deseadan

Platypittamys (Wood, 1949) is amazingly similar to that of *Octodon* itself (with which Wood did not have an opportunity to compare it), considering the vast time interval between the two. The chief differences lie in the proportions of the hind limb elements, and even these are not great. The tibia and fibula and the metatarsals are somewhat longer in the Recent form. The intersegmental indices of *Octodon* are: humerus/radius = 1.06; femur/tibia = 0.83; intersegmental index, $\frac{R + H}{T + F} \times 100 = 67.3$; the corresponding figures for *Platypittamys* (Wood, 1949, pp. 42-43) are 1.04, 0.99 and 67.0. The tibia and fibula remain separate in *Octodon* as in *Platypittamys,* as indeed they do in many caviomorphs. In old individuals in several families, the expanded proximal portion of the fibula fuses with the tibia, but, in all skeletons we have examined, the distal ends are separate. We interpret fusion of either end of these bones, then, as a progressive character of the modern Caviomorpha (whatever it may have been in the Old World forms). We feel that the distribution of proximal fusion of these bones within the suborder very clearly demonstrates that the two bones were separate in the ancestral stock, a conclusion diametrically opposed to that reached by Landry (1957a, p. 19). It would appear that, apart from the hypselodont cheek teeth, *Octodon* and other nonfossorial octodontids are among the most generalized of living caviomorphs.

It must also be noted (see below, p. 300) that the Acaremyinae of Ameghino, Scott and others (Wood's Acaremyidae) included a number of forms that are in reality members of the very closely related Echimyidae. We may also note in passing that the supposed Colhuehuapian octodontid *''Eoctodon''* is also an echimyid (see p. 302), and not an ''acaremyine'' as stated by Landry (1957a, pp. 39 and 56).

On the basis of his study of *Platypittamys,* Wood concluded that the ''Acaremyidae'' were ancestral, at least structurally, to all rodents here included in the Caviomorpha, with the possible exception of the Erethizontidae. This conclusion stands unchanged, except that the word ''Acaremyidae'' must be replaced by ''primitive Octodontidae.''

PLATYPITTAMYS Wood

Platypittamys Wood, 1949, p. 5.

PLATYPITTAMYS BRACHYODON Wood

P. brachyodon Wood, 1949, pp. 6-43, Figs. 1-6, 8.
P. brachydon (*sic*), Landry, 1957a, pp. 92, 93.

Horizon and locality. Deseado formation; Scarritt Pocket, Rinconada de los Lopez, Chubut.

This genus has been described in detail by Wood, and there is no need to repeat his account. This opportunity is taken to point out that he erroneously labeled Figure 3C as left instead of right and Figure 3D as right instead of left.

The work reported on here and studies of later octodontids (Patterson and Kraglievich ms.) necessitate some discussion of the previous interpretation of P^4. The pattern of this tooth in *Platypittamys* is such that it could not have been derived from that of any described paramyid except by considerable reduction or degeneration. A recently discovered but still undescribed lower Gray Bull paramyid, however, has a premolar that could readily have given rise to that of *Platypittamys;* this suggests the possibility that there has been no secondary reduction in P^4 of the Caviomorpha.

By comparison with later members of the family, a terminology of the parts of the premolar has been adopted with the avowed intention of making the premolar terminology of the later octodontids agree with that of the molars, with the full understanding that the homologies suggested may be incorrect. This may or may not be phylogenetically justifiable, but is certainly convenient.

On this basis, we now interpret the premolar of *Platypittamys* as having a lingual protocone, and a buccal paracone and metacone, widely separated, the former incorporated in the protoloph and the latter in the posteroloph. No trace of a separate metaloph is present. There is a well-developed anterior cingulum, approaching the stage where it would be called an anteroloph. The Santacruzian *Sciamys* shows that the metaloph in octodontids was a later addition to the premolar crown that arose as a low, inconspicuous ridge on the anterior slope of the posteroloph.

Available evidence strongly suggests that in all caviomorphs the metaloph is the last of the premolar crests to come into existence, being formed in some groups by a progressive division of the posteroloph that begins with the development of a minute fossette in this crest.

Wood regarded the single posterior crest of P_4 of *Platypittamys* as the hypolophid. Conditions in *Sciamys* tend to confirm this interpretation. In that genus, some examples of P_4 occur in which the talonid is as simple as that of *Platypittamys;* others show various stages in the formation of a posterolophid by development of a cingulum posterior to the internal half of the hypolophid. In one individual (M.A.C.N. no. A 1879), however, the entoconid is connected to the ectolophid by a crest anterior to, and obviously formed later than, that joining the entoconid to the hypoconid. Development of a notch posterior to the entoconid in this specimen would have converted what is clearly the equivalent of the hypolophid in other individuals into a posterolophid. Such differences are trivial but they do show that the two talonid crests of the caviomorph P_4 could have arisen in different ways in various groups. Conditions in P_4 of the Deseadan cavioid *Asteromys* in fact suggest that the hypolophid arose in a manner comparable to that of the anterior crest in the aberrant *Sciamys* just discussed.

On the other hand, there still remains the possibility that there is no direct connection between the undescribed Gray Bull form and *Platypittamys*, in view of the very considerable time gap. A gap of this size is certainly too large to permit phylogenetic conclusions to be drawn with any confidence. The possibility should not be lost sight of that P^4 of *Platypittamys* is secondarily simplified. Such a simplification would not be entirely unexpected, and the possible sequence of events would be as outlined in the following paragraphs.

Among various groups of rodents, there has quite obviously been reduction of the premolars. In no known rodents are there more than two upper and one lower premolars. No one doubts that this is a reduction from the primitive placental formula. A premolar formula of $\frac{2}{1}$ is retained by only a few rodents, including most of the typically Eocene Ischyromyoidea, and the Sciuridae. Many other rodents show varying traces of reduction, to P^1_1 or P^1_0, before we reach the cricetid and murid condition of P^0_0. We explicitly accept this dental formula for these families, without any prejudice as to other families where dm^4_4 may have been retained and M^3_3 lost, which is surely not true of the Muroidea. The Caviomorpha retain one upper and one lower premolar. They must, therefore, have lost the third upper premolar, which is present in the paramyids.

Obviously, there must have been a reduction of the premolars, in the Paleocene rodents, giving us a paramyid condition by the late Paleocene. There was then a halt in the reduction, until middle Eocene or later, when a number of groups continued the reduction of premolars, first losing P^3, then P_4, and finally P^4. It seems evident to us that this tendency to lose premolars must have been accompanied by a simplification of the pattern before the loss took place.

According to this interpretation, the premolars of *Platypittamys* (especially P^4) would represent a simplification from the *Paramys* pattern, which was followed by a secondary redevelopment of complexity in this tooth in the later Caviomorpha. While this would be a case of reversibility of an evolutionary trend, it nevertheless is still an entirely logical explanation of what happened among the Caviomorpha.

Platypittamys is extraordinarily primitive, for a caviomorph, in the small size of the infraorbital foramen. The two available specimens are both badly crushed but, despite this, the structure of the zygomasseteric region can be determined with reasonable assurance. The foramen can hardly have been appreciably larger than shown in Wood's figure (1949, Fig. 2). Landry (1957a, p. 93), reports that he was unable to confirm Wood's account of the size of this structure, stating that "if this is true, Wood has here an exact intermediate in zygomasseteric structure between the ischyromyids and one of the three advanced groups, something no one else has ever been able to find." An independent check of the specimens by both of us, however, has convinced us that Wood was correct in his interpretation. Perhaps some of Landry's difficulty in visualizing what has happened in the crushing of this part of the fossil may be explained by the fact that he has confused M^3 and P^4. As a result, a shifting of the palate to restore the break and to put M^3 in its proper place would move the lateral wall of the infraorbital foramen much less than would have been the case if Landry had been correct and the tooth had been P^4. The fact that there is no definitely marked area on the mandible for the insertion of M. masseter medialis, pars anticus, is in accord with the small size of the foramen, since it indicates that this division of the muscle (which is the one that passes through the foramen) was at best poorly developed. A recheck of the specimen again confirms Wood's statement that the masseter was apparently limited to the ventral surface of the zygoma, since there is no suggestion that any part of the muscle passes through the foramen. As Landry states (1957a, p. 93), the specimens are so crushed that it cannot be told whether the muscle had invaded the orbit. The contemporary *Cephalomys,* the only other Deseado rodent for which we have any knowledge of the skull, has an enormous infraorbital foramen, relatively larger than in its much later relative *Neoreomys*. It is very possible therefore that *Platypittamys* was a persistently primitive, little-modified survivor, in this respect at least, of the basic immigrant stock. In the Colhuehuapian species of *Acaremys* there is a well-defined area of insertion on the mandible for M. masseter medialis, pars anticus, indicating that this part of the muscle, and hence presumably the foramen through which it passed, was nearly, if not quite, as developed as in the Santacruzian species. Landry (1957a, pp. 93-94) questions whether it is likely that the enlargement of the foramen took place independent of the movement of the muscle. We agree that this independence of development may seem improbable, but the evidence seems to indicate that it took place.

As stated by Wood (1949, p. 29), there is an entepicondylar foramen on the humerus, and the proximal ends of the tibia and fibula are not fused (*op. cit.,* p. 36), which makes it difficult to accept Landry's thesis that the primitive "hystricomorphs" were characterized by proximal fusion of the tibia and fibula and by loss of the entepicondylar foramen (Landry, 1957a, pp. 19, 20).

The suggestion has been made that the Scarritt Pocket, in which *Platypittamys* occurs, may be somewhat older than the other Deseadan local faunas of Patagonia, but this does not now appear to be the case. The evidence strongly suggests that these faunas were all very nearly of the same age, since there is no indication of evolutionary change from one to another.

Platypittamys is the only known Deseadan octodontid. The family is actually a rare one in the Oligocene and Miocene. Only the Santacruzian *Sciamys* is reasonably common, and there are but four known specimens from the earlier horizons. The relatively abundant Colhuehuapian *Protacaremys*, as noted below, is not an octodontid, but an echimyid. A tentative approximation of a phylogeny of the Miocene and earlier forms is shown in Figure 2.

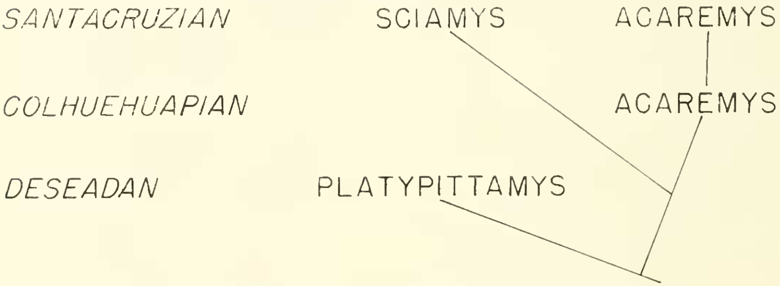

Fig. 2. Tentative phylogeny of the Oligocene and early Miocene Octodontidae.

Family ECHIMYIDAE Miller and Gidley 1918

The earliest Echimyidae are very similar to the earliest Octodontidae in molar structure, so much so that several of them have been placed in the latter family (in the guise of "Acaremyinae") by Ameghino, Scott and others. The similarities are so close that we have no hesitation in referring them to the same superfamily. Landry (1957a, p. 56) separates the two families widely, placing the Echimyidae in his Erethizontoidea. We feel that this disagreement is to some degree more apparent than real, since he, in common with most other authors, refers the earlier octodontids, as "Acaremyinae," to the Erethizontidae, and between these early octodontids and the early echimyids there is a very close affinity. Landry includes *Capromys* and its relatives as a subfamily of the Echimyidae and separates the nutrias (*Myocastor*) as a distinct family, which he places in the Octodontoidea. The echimyids and capromyids seem to be definitely related, and we believe that the nutrias also belong in the same major group, although we have no strong feelings as to the precise taxonomic rank that should be given them. Study of post-Deseadan members of the Echimyidae and Octodontidae (Patterson and Kraglievich, ms.) has revealed that the Colhuehuapian *Protacaremys* and "*Acaremys*" *preminutus*, and the Santacruzian "*Acaremys*" *minutus* and "*A.*" *minutissimus* and "*Sciamys*" *tenuissimus* are all echimyids. The molars of these forms may be distinguished from those of octodontids by the deeper anterior and posterior fossettes and fossettids, the somewhat more oblique lophs and lophids, the somewhat deeper paraflexus and metaflexid, a marked tendency toward reduction and loss of the metalophid (starting with M_3), and by the somewhat greater length as compared to width of unworn crowns. The most obvious difference in the dentition lies, however, in the retention of dm$_4^4$ and the suppression of P_4^4. This was first pointed out by Friant (1936a), who noted that in certain Recent and Pleistocene forms the anterior cheek tooth is invariably more worn than the molars and that there is no evidence that it was ever replaced. The abundant material examined by Patterson and Kraglievich shows that this is also true for all Tertiary forms from the Colhuehuapian on. From one Santacruzian specimen, they were even able to extract the crown of a premolar, of the *Acaremys* type, from deep within the ramus, below the first lower cheek tooth. It is virtually certain that this tooth would never have erupted.

Four Deseadan specimens, representing two distinct species of a new genus, *Deseadomys*, are certainly referable to this family on the basis of molar structure. The anterior cheek tooth is preserved in two of them and in both it is clearly an octodontid-like premolar and not a milk molar. This suggests that retention of dm$_4^4$ in the Echimyidae came about between Deseadan and Colhuehuapian time.

The phylogeny of the Echimyidae was evidently very complex, and the available material is insufficient to trace it in any great detail. A tentative phylogeny, however, is given in Figure 3, adapted from Patterson and Kraglievich (ms.). *Deseadomys* seems to be ancestral to the comparatively specialized *Adelphomys* group, composed of the Santacruzian *Adelphomys* and *Stichomys* and an undescribed Colhuehuapian genus, but not including *Protadelphomys.* The molars of *Deseadomys* are actually higher crowned than those of the Colhuehuapian *Protacaremys* and *Prospaniomys.* These last are sufficiently similar to suggest that their common ancestors may have lived in Deseadan time. The primary radiation of the Echimyidae was evidently in progress during the Deseadan and presumably had begun not long prior to it. Derivation from the primitive octodontid stem is clearly indicated. The Colhuehuapian *Eoctodon* Ameghino is neither valid nor an octodontid. The type species, *E. securiclatus,* is a synonym of *Protacaremys prior* and the larger *E. crassiusculus* is a synonym of *Prospaniomys priscus.* Both these forms are echimyids. The Santacruzian *Spaniomys* is highly variable, and *Gyrignophus complicatus* and *Graphimys provectus* appear to have been based on extreme variants of *S. modestus.*[5]

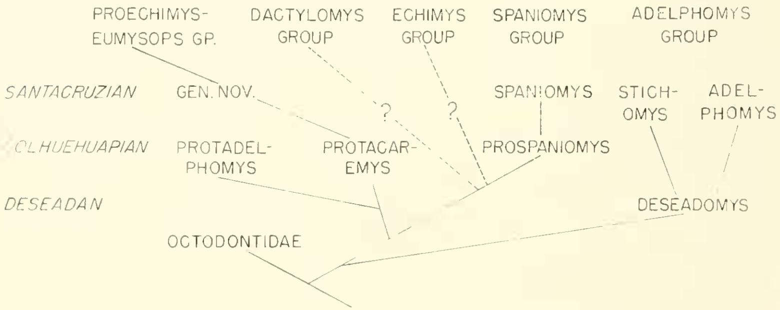

Fig. 3. Tentative phylogeny of the Oligocene and early Miocene Echimyidae.

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[5] J. L. Kraglievich (1957, p. 37) believes the "*Eumysops* group" (cf. Fig. 3) to be part of the subfamily Heteropsomyinae Anthony. The Pliocene genera *Proatherura* and *Proaguti* of Ameghino cannot be separated from *Eumysops.*

Deseadomys gen. nov.

Asteromys Loomis, 1914, pp. 194-195 (in part), *nec* Ameghino 1897c; Wood, 1949, pp. 4, 15, 16, 18-20; Schaub *in* Stehlin and Schaub, 1951, p. 60.

Type species. D. arambourgi sp. nov.

Distribution. Deseadan; Patagonia.

Diagnosis. Differing from all other known echimyids in replacement of dm$^4_4$ by P$^4_4$; cheek teeth mesodont, lower crowned than in *Adelphomys* and *Stichomys,* higher crowned than in *Protacaremys* and *Prospaniomys,* with unilateral hypsodonty in uppers but not in lowers; P^4 (known only in type species) not molariform, without metaloph, protoloph concave anteriorly; M^3 (known only in type species) more circular in outline and with hypocone less internal than in *Adelphomys* and *Stichomys;* P$_4$ (known only in type species) not molariform, without anterolophid, metaconid separated from protoconid by narrow cleft, metalophid rudimentary; lower molars more advanced in metalophid reduction than in *Protacaremys* and *Prospaniomys.*

A second species, *D. loomisi* sp. nov., somewhat more advanced than the type, is referred to the genus. The two species appear to have been trending toward the two Santacruzian genera, the type toward *Stichomys* and *D. loomisi* toward *Adelphomys.*

Deseadomys arambourgi[6] sp. nov.

Figs. 4-6

Asteromys prospicuus Loomis, 1914, p. 195 (in part), Fig. 128 (*nec* Ameghino 1897c); Schaub *in* Stehlin and Schaub, 1951, p. 60, Fig. 72.

Type. M.N.H.N. no. 1903-3-1, right mandible with I, P$_4$-M$_3$.

Hypodigm. Type and A.C.M. nos. 3163, right P^4-M^2 (described and figured by Loomis as *Asteromys prospicuus*)[7] and 3071, left M^3.

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[6] Named for Professor Camille Arambourg, as a slight return for his kindness in entrusting to us the Deseado rodents in his charge.

[7] These three teeth are isolated with no trace of connecting bone. They were, however, associated in the field (Loomis, personal communication to Wood, February, 1935) and presumably represent a single individual. Loomis' figure shows four teeth. The one figured by him as M^3 has a wear facet on both the front and the rear, proving it to be one of the central molars. On the basis of wear, it is interpreted as M^2 and Loomis' M^2 as M^1. The tooth figured by him as M^1 is not in the Amherst collections, and was apparently lost sometime between Loomis' description of the material in 1914 and Wood's visit to Amherst in 1935. As the specimen was mounted, there was a space between P^4 and Loomis' M^2 (our M^1), where a tooth obviously had been, and whence it had been lost.

Horizon and localities. Deseado formation; La Flecha, Santa Cruz (type), Cabeza Blanca, Chubut (Amherst specimens).

Diagnosis. Metalophid absent on M_3, interrupted on M_2, present on M_1; teeth somewhat lower crowned than in *D. loomisi.*

Loomis' reason for referring A.C.M. no. 3163 to *Asteromys*, whose upper dentition is not certainly known, presumably lay in his identification of an isolated cheek tooth (A.C.M. no. 3054), shown in his Figure 129, as M_2 of *A. prospicuus.* This species, as pointed out below, is actually a synonym of *Cephalomys plexus;* A.C.M. no. 3054 is not referable to it. The specimen appears to be an upper cheek tooth of an eocardiid, perhaps, although not surely, of *Asteromys punctus,* which is without question a member of this family (see below, p. 376). Since A.C.M. no. 3054 does show a certain resemblance to the lower molars of *A. punctus,* which were figured by Ameghino, Loomis' generic identification of it was as good as he could have made. As regards the specific identification, he should have noted that his tooth was much larger than Ameghino's syntype specimens of "*A. prospicuus.*" The small, ephemeral mesofossette of A.C.M. no. 3054 definitely excludes the specimen from the Echimyidae and Octodontidae. The reference of the upper cheek teeth, A.C.M. no. 3163, to the same species as no. 3054 was presumably made chiefly on the basis of size, general similarity, and occurrence in the same deposit. It was, however, definitely erroneous. Having made it, Loomis went on to observe the close general resemblance between the cheek teeth of A.C.M. no. 3163 and those of "*Acaremys*" *minutus* and *minutissimus*[8] figured by Scott, and to conclude that "*Asteromys* appears to be the direct ancestor of *Acaremys.*" Unfortunately, as already noted, "*A.*" *minutus* and *minutissimus* are not octodontids ("acaremyines"), as Ameghino and Scott supposed, but echimyids. As a result of this cumulative series of errors, *Asteromys* has been, since 1914, listed as a member of the "Acaremyidae" or Erethizontidae, "Acaremyinae."

A.C.M. no. 3163 is certainly an echimyid, possessing every one of the molar characters mentioned above that separate the early members of this family from the early Octodontidae. Our

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[8] Loomis did not specifically mention these species, but they are the only ones among those referred to *Acaremys* by Scott for which crown details are shown, and it is to Scott's publication that he would obviously have turned.

reasons for referring the specimen to *Deseadomys arambourgi* are as follows: the teeth are higher-crowned than those of the Colhuehuapian *Protacaremys* and *Prospaniomys*, and in this feature and in crown structure resemble the *Adelphomys* group; the lower molars of *Deseadomys* definitely resemble those of the *Adelphomys* group in both height and structure; within this group A.C.M. no. 3163 is closer to *Stichomys* than to *Adelphomys* in molar structure; the same is true of the lower molars of *D. arambourgi;* A.C.M. no. 3163 and the type of *D. arambourgi* agree perfectly in size. The two specimens are from different localities — Cabeza Blanca and La Flecha, respectively — but this is no obstacle to regarding them as conspecific, since many species, among them rodents, are common to both.

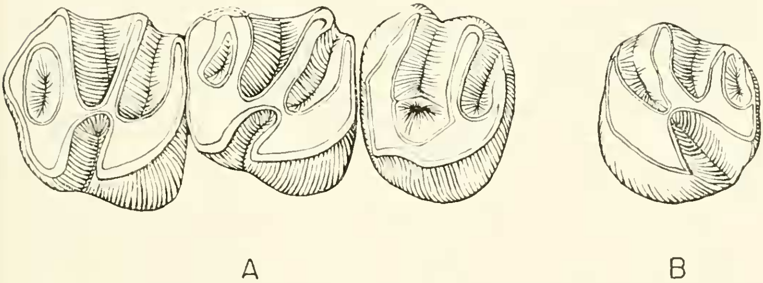

Fig. 4. *Deseadomys arambourgi* gen. et sp. nov. x 10. *A*, RP^4-M^2, A.C.M. no. 3163; *B*, LM^3, A.C.M. no. 3071.

P^4 is considerably smaller, simpler and more oval in outline than the molars (Fig. 4A). The anteroloph runs outward from the large protocone for about two-thirds of the way across the anterior face of the tooth, falling well short of the paracone. The protoloph is slender and somewhat concave anteriorly. As in *Platypittamys*, there is no trace of a metaloph. The posteroloph forms the posterior third of the tooth. This crest differs from that of *Platypittamys* in that there is a definite enlargement at the postero-internal corner, so that we may consider that there is a hypocone as well as a metacone in the posteroloph. The paraflexus is rather shallow, the mesoflexus deep. The protocone and hypocone are only very slightly separated, there being a faint groove on the lingual face indicating incipient separation. It is too faint to be called a hypoflexus. Near the middle of the tooth, there are crests extending into the mesoflexus from both the protoloph and the posteroloph, which partially dam the mesoflexus (and would split it in half at an advanced stage of wear). These crests seem to suggest the initial stages of a mure, as in the molars, but it seems clear that the molar pattern was not developed in this manner, but rather by a deepening of the hypoflexus until the connection between the protocone and hypocone came to lie near the center of the tooth. The tooth is definitely more advanced than P^4 of *Platypittamys*, but the advances were of no significance for the later history of the family, the premolars being destined to disappear from the functional dentition.

M^{1-2} (Fig. 4A) have the usual four transverse crests which are longer and more lophate than in *Platypittamys*. The anteroloph is better developed than in P^4, but does not extend as far externally as does the protoloph. The latter crest is thin and inclined anteriorly, markedly so on M^1. It is united with the anterior end of the mure rather than directly with the protocone, to which it is connected by a thin isthmus. The metaloph and posteroloph unite externally at an early stage of wear to enclose a metafossette that is worn away before the mesoflexus is isolated to form a fossette. The paraflexus is more widely open than in early octodontids, but would be isolated to form a lake while the deep lingual end of the metafossette was still present. The mesoflexus is widely open, but would ultimately be converted to a mesofossette. The hypoflexus is of nearly uniform depth throughout so that it might never be converted to a fossette. The protocone is elongate anteroposteriorly. These teeth closely resemble those of *Stichomys* and *Adelphomys*, and agree with those of *Stichomys* in all characters in which they differ from those of *Adelphomys*. These differences are: anteroloph not extending as far externally as the protoloph; paraflexus notably shallower than mesoflexus; metafossette relatively large and persistent; hypoflexus deep and persistent. The hypoflexus does not extend as far externally into the base of the protoloph in all molars of *Descadomys* as it does in the Santacruzian forms.

M^3 (Fig. 4B) is slightly smaller and has a rounder outline than its predecessors. The metaloph and posteroloph are just in process of uniting, so that decision as to whether there is a metaflexus or a metafossette is purely a matter of terminology. There was clearly a metaflexus at an earlier stage of wear. The hypocone is quite external in position, more so than in *Platypittamys*, and the posterior portion of the tooth is notably smaller than the anterior. *Adelphomys* has a smaller, less elongate M^3 than *Stichomys*, a point of resemblance to *Deseadomys* and presumably a primitive feature. *Stichomys* resembles the Deseadan form in nearly all details of crown structure, including the presence of a metaflexus.

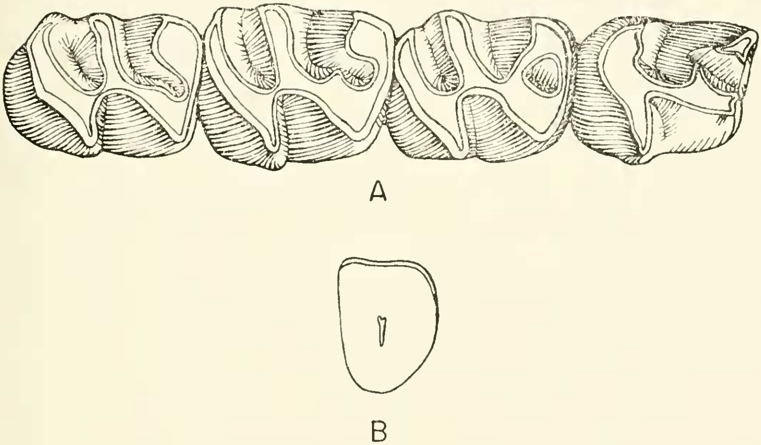

Fig. 5. *Deseadomys arambourgi* gen. et sp. nov. x 10. Type, M.N.H.N. no. 1903-3-1. *A*, RP_4-M_3; *B*, cross-section of RI_1, posterior view.

The lower premolar (Fig. 5A) is very similar to that of *Platypittamys* (Wood, 1949, Fig. 3 C, D), but is slightly less molariform. The protoconid is connected with the center of the hypolophid by a nearly straight, slightly obliquely directed, and nearly centrally located ectolophid, as in *Platypittamys*. The hypolophid forms the posterior margin of the crown, uniting the prominent anteroposteriorly compressed hypoconid with the very large and more rounded entoconid. As in *Platypittamys*, there is no suggestion that more than one crest is present at the rear of the tooth. Anteriorly, the protoconid sends a blunt spur linguad —the rudiment of the metalophid. The metaconid is a stout, four-sided cusp, separated from the protoconid by a narrow, fairly deep mesoflexid. With extreme wear, the central part of this would form a mesofossettid, as it does in a much earlier stage of wear in *Platypittamys*. The posterior corner of the metaconid is formed by a very short, blunt spur that projects in the direction of the tip of the metalophid rudiment. There is no anterolophid, nor any indication of a mesoconid or mesolophid. External and internal valleys are long and of nearly equal length.

The lower molars are longer relative to width than those of *Platypittamys* and are considerably more specialized in the reduction and loss of the metalophid, which is progressive from M_1 to M_3 (Fig. 5A). On M_1, this crest is short, inclined more anteriorly than in *Platypittamys* and joined to the internal rather than to the posterior face of the metaconid. On M_2, it is interrupted, being represented only by a short, blunt spur from the protoconid, which would unite with the metaconid only after extreme wear. On M_3, the metalophid is extremely reduced, and barely present at all. It would never reach the metaconid. A tendency toward reduction and loss of the metalophid occurs sporadically in caviomorphs. It is characteristic of echimyids, occurs in the later members of the Luantinae among eocardiids, in the *Capromys* group of capromyids, and may be seen in a few individuals of the octodontid *Sciamys*. This crest is the weakest of the four on the lower molars (as Wood noted [1949, p. 21], the anterolophid provides the main connection between protoconid and metaconid), and this no doubt accounts for the tendency toward loss. Curiously enough, there is a compensatory tendency in the *Proëchimys-Eumysops* group of echimyids for a neolophid to arise in place of the metalophid subsequent to its disappearance.

The deep hypoflexid is much less oblique than in *Platypittamys* — a point of resemblance to *Stichomys* and *Adelphomys*. The internal flexids are wider, due in part to the reduction of the metalophid and in part to the greater length of the teeth relative to width. The mesoflexid is vertically the deepest of the valleys, being slightly deeper than the hypoflexid, and is of essentially even depth throughout its course. The narrower metaflexid is shallower but deepens sharply buccad, so that a metafossettid would be isolated by further wear. The posterolophid is made up of the hypoconid and the posterior cingulum. There does not seem to be any swelling of this crest that could reasonably be considered to be the entoconid. The hypolophid therefore must contain the entoconid at the lingual margin of the tooth. In the upper Eocene paramyid *Rapamys* (Wood, 1950, Fig. 2B), there is a hypolophid extending from the entoconid to the anterior corner of the hypoconid at the point where the ectolophid arises. Apparently, with the gradual reduction of the metalophid, the entoconid and particularly the buccal end of the hypolophid have swung forward, giving the diagonal direction to this crest that characterized *Deseadomys*, where the hypolophid joins the ectolophid rather than the hypoconid. With the reduction of the metalophid, there is a corresponding increase in the width of the flexids. As in *Stichomys* and *Adelphomys*, there is no tendency toward unilateral hypsodonty. The depths of the hypoflexid and mesoflexid and the shallowness of the metaflexid relative to the mesoflexid are points of resemblance to *Stichomys*. In this genus, there is no trace of a metalophid on M_{2-3}, but in approximately a third of the specimens in the Ameghino Collection this crest is present, although very small, on M_1, connecting the protoconid with the junction of the anterolophid and metaconid.

The incisor (Figs. 5B, 6) is moderately stout and extends back to a point beneath M_3. The anterior face is nearly flat, but has a very faint longitudinal sulcus down the center, which is probably an individual peculiarity, since such faint sulci are very variable in many groups of rodents, including both the Paramyidae and the Santacruzian Echimyidae. The enamel extends for over a third of the way around on the outer side and is barely reflected over to the inner. In cross-section, the pulp cavity is elongate. The incisor of *Stichomys* has a much more curved anterior face.

The mandible (Fig. 6) is robust, deep through the masseteric fossa and symphysis, and the symphyseal region is elongate, extending back to a point beneath P_4. The genioglossal pit is poorly marked. The masseteric fossa begins beneath the posterior part of M_1 and the ventral margin is markedly everted, so that the fossa is deep; there is almost no dorsal boundary. The specimen is broken in the region of the angle and it is therefore impossible to say whether or not this was inturned, although it presumably was. The coronoid arises near the front of M_3. The mental foramen is about a third to a half of the way down the side of the mandible, about the middle of the diastema. The chin is slightly indicated. The symphysis shows very minor irregularities, and it seems probable that some movement between the two halves of the jaw was possible and that a small M. transversus mandibulae was present. In nearly every respect, the jaw closely resembles those of *Stichomys* and *Adelphomys.*

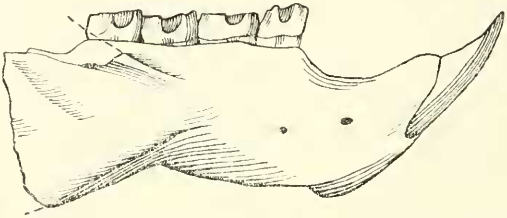

Fig. 6. *Deseadomys arambourgi* gen. et sp. nov. x 3. Type, M.N.H.N. no. 1903-3-1, right ramus, lateral view.

Apart from slight differences in the general shape of the incisor and in the contour of its anterior surface, *D. arambourgi* resembles *Stichomys* very closely. Since development and loss of shallow sulci and changes in the shape of the incisor may occur frequently in rodents, it is even possible that this species may be in the direct ancestry of the Santacruzian genus.

For measurements, see Table 1.

DESEADOMYS LOOMISI[9] sp. nov.
Fig. 7

Type. A.C.M. no. 3087, right mandible with I, M_{1-2}, alveoli of P_4, M_3.

Hypodigm. Type only.

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[9] Named for the late Professor Frederick B. Loomis, who organized and led the Amherst Patagonian Expedition of 1911-12.

Horizon and locality. Deseado formation; Cabeza Blanca, Chubut.

Diagnosis. Metalophid entirely absent; teeth slightly larger and molars somewhat higher-crowned than in *D. arambourgi;* mesoflexid deeper than in *D. arambourgi;* metaflexid fairly shallow, so that lingual ends of hypolophid and posterolophid approach more closely than in *D. arambourgi.*

The cheek teeth (Fig. 7A) are medium-crowned, but, as in *Adelphomys* and *Stichomys,* show no indications of unilateral hypsodonty. As in the type species, M$_2$ is the largest tooth. M$_3$ (as determined from the alveolus) was the smallest of the series. P$_4$ appears to have been about the size of M$_1$, which is an advanced character. There is no trace in either molar of any remnants of the metalophid, so that the teeth are entirely three-lobed on the lingual side. The mesoflexid and hypoflexid are about equally deep, and much deeper than the metaflexid. With wear, the metafossettid would persist until after the formation of the mesofossettid and hypofossettid, but would be worn away shortly thereafter. The hypofossettid is slightly deeper than the mesofossettid.

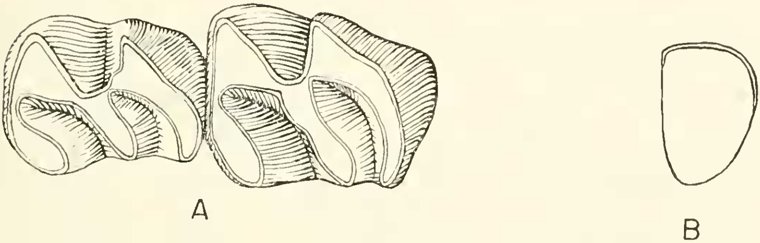

Fig. 7. *Deseadomys loomisi* sp. nov. x 10. Type, A.C.M. no. 3087. *A,* RM$_{1-2}$; *B,* cross-section of RI$_1$, posterior view.

The anterior face of the lower incisor is straight for the median two-thirds and gently curved on the buccal third (Fig. 7B). There is no suggestion of a sulcus. The enamel extends nearly halfway around the buccal side of the tooth, but only a short distance onto the lingual face. The two sides of the tooth are nearly parallel, as in *D. arambourgi.* The pulp cavity is long and narrow, but its details could not be determined. The incisor extends back to beneath M_2, thus not as far as in *D. arambourgi*. The lower incisor in *Adelphomys* is relatively larger, wider, and has a plane anterior surface.

The mandible differs from that of the type species in that the anterior end of the masseteric crest is beneath P_4 instead of M_1. This is a primitive character encountered in octodontids, *Protacaremys, Prospaniomys,* etc. The symphyseal surface is essentially plane.

As far as the available evidence goes, there is nothing to oppose the view that *D. loomisi* was in or near the ancestry of *Adelphomys*.

The tooth measurements are given in Table 1.

TABLE 1

Tooth measurements (in mm.) of *Descadomys*

Upper Teeth			Lower Teeth			
		D. arambourgi A.C.M. no. 3163, right			*D. arambourgi* M.N.H.N. no. 1903-3-1, right	*D. loomisi* A.C.M. no. 3087, right
P^4,	anteroposterior	2.09	Incisor			
	width protoloph	2.03*		anteroposterior	1.76	ca. 1.9
	width posteroloph	2.12*		transverse	1.31	1.29
M^1,	anteroposterior	2.25	P_4	anteroposterior	2.12	
	width protoloph	2.25*		anterior width	1.68*	
	width metaloph	2.04*		width hypolophid	1.90*	
M^2,	anteroposterior	2.42	M_1	anteroposterior	2.41	2.63
	width protoloph	2.61*		width metalophid	1.92*	2.10*
	width metaloph	2.41*		width hypolophid	1.96*	1.92*
		A.C.M. no. 3071, left	M_2	anteroposterior	2.52	2.64
				width metalophid	2.05*	2.47*
M^3,	anteroposterior	2.14		width hypolophid	2.18*	2.29*
	width protoloph	2.35*	M_3	anteroposterior	2.32	
	width metaloph	1.88*		width metalophid	1.90*	
				width hypolophid	1.89*	

* = Maximum diameter of tooth.

Superfamily CHINCHILLOIDEA L. Kraglievich 1940

As discussed below under Dasyproctidae (p. 327), we now suspect that a number of caviomorph families should be included in this superfamily.

Family CHINCHILLIDAE Bennett 1833

SCOTAMYS Loomis 1914

Scotamys Loomis, 1914, p. 192; Stehlin and Schaub, 1951, p. 260.

Type species. Scotamys antiquus Loomis 1914.

Distribution. Deseadan; Patagonia.

Emended diagnosis. Teeth very high-crowned, apparently rootless and ever-growing; crown pattern rapidly lost; hypoflexus and hypoflexid very deep; small third lobe on unworn upper molars; enamel missing from anterior part of lower molars and posterior part of uppers after little wear; cement present; incisors proportionately small.

SCOTAMYS ANTIQUUS Loomis 1914

Figs. 8-10

Scotamys antiquus Loomis, 1914, p. 192-193, Figs. 125-126; Stehlin and Schaub, 1951, Fig. 434, p. 260.

Type. A.C.M. no. 3063, a left lower jaw with I, P_4-M_2, from Cabeza Blanca, Chubut.

Hypodigm. Type and a series of isolated teeth in collection of Muséum National d'Histoire Naturelle (3 P^4, 15 $M^{1 \text{ or } 2}$, 3 M^3, 3 P_4, 9 $M_{1 \text{ or } 2}$, 1 M_3 and 11 incisors), all from La Flecha, Santa Cruz.

Diagnosis. As for the genus; tooth measurements as shown in Table 2.

It is often very difficult to determine with certainty the position in the tooth row of the isolated teeth. The patterns of P^4, M^3 and P_4 are sufficiently distinctive so that these teeth can be readily identified. M_3 can, we believe, be identified by the narrow talonid. $M^{1\text{-}2}$ cannot be separated from each other, as is also the case with $M_{1\text{-}2}$. The upper molars have a greater curvature of their vertical axes, both anteroposteriorly and transversely, than do the lowers, and the two have been separated on this basis. The interruption of the enamel in upper molars is generally the mirror image of that in the lowers.

No unworn cheek teeth are available. The general resemblance between *Scotamys* and the better known *Cephalomys* is sufficiently close, however, so that it seems justifiable to interpret such structure as can be seen in the former in terms of the latter.

P^4 (Fig. 8A) has a very large combined anteroloph and protocone that, together, forms all of the anterior and much of the external and internal faces of the tooth. This curving crest is separated from the paracone and its crest by a cleft, the hypoflexus, that extends nearly to the buccal margin of the tooth, though, in contrast with the situation in *Cephalomys,* it is open at the lingual end. This lingual opening does not extend far down the tooth, however, so that, with wear, the valley becomes a fossette, as in *Cephalomys.* The paracone is central in position and continues into a short crest, the protoloph, that describes a curve similar to that of the much larger anteroloph. The metacone is posteroexternal and united by wear to the paracone. A narrow crest, the posteroloph, runs internally from the metacone, forming the posterior margin of the tooth and joining the protoloph posterointernally. A small, shallow mesofossette is isolated between protoloph and posteroloph. Metacone, mesofossette and posteroloph are situated on a posteriorly overhanging portion of the crown, so that all trace of these structures disappears after

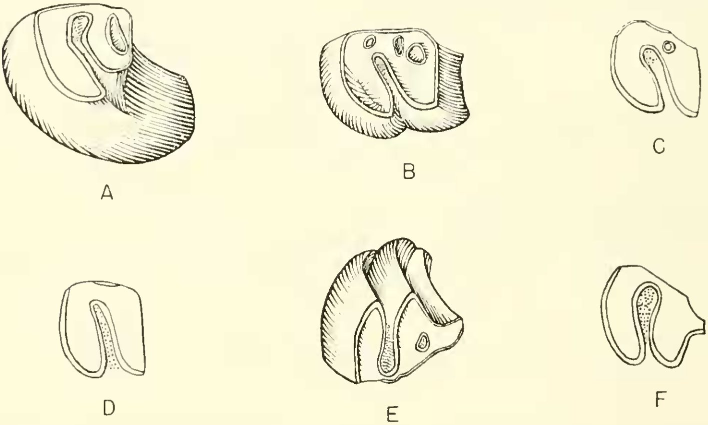

Fig. 8. *Scotamys antiquus* Loomis x 5. *A,* LP^4, M.N.H.N. no. 1903-3-8; *B,* $LM^{1 \text{ or } 2}$, M.N.H.N. no. 1903-3-9; *C,* $LM^{1 \text{ or } 2}$, M.N.H.N. no. 1903-3-10; *D,* $LM^{1 \text{ or } 2}$, M.N.H.N. no. 1903-3-11; *E,* RM^3, M.N.H.N. no. 1903-3-12; *F,* LM^3, M.N.H.N. no. 1903-3-13. *C, D* and *F* show crown outlines at wear surface.

a little wear, leaving a bilobed crown that then persists until after the closure of the hypoflexus. There is no indication that a metaloph was ever present. The enamel is interrupted early in life at the postero-buccal corner of the tooth, and then along the rest of the buccal side.

The least worn $M^{1 \text{ or } 2}$ in the series (M.N.H.N. no. 1903-3-9, Fig. 8B) shows a pattern consisting of two lobes separated by a narrow hypoflexus that extends about three-quarters of the way from the lingual to the buccal margin. Buccad of the hypoflexus is a small fossette and in the buccal portion of the posterior lobe are two more. All three are shallow. The anterior is the smallest, the middle the deepest, and the posterior the largest. From these remnants, the unworn crown pattern can readily be reconstructed. It was clearly very similar to that of the unworn *Cephalomys* molar without the fifth crest, consisting of a large anteroloph, a stout protoloph, a metaloph that was more transverse than in *Cephalomys*, a posteroloph and a hypoflexus that undermined the paraflexus (i.e., the paraflexus extended more linguad on the unworn crown than was the case farther down in the tooth, so that, as wear proceeded, the paraflexus diminished in length and the hypoflexus increased). Thus interpreted, the three fossettes in M.N.H.N. no. 1903-3-9 are the parafossette, mesofossette and metafossette. A basic similarity to the *Platypittamys-Deseadomys* pattern is evident. The posteroloph protrudes beyond the main body of the tooth and is soon eliminated by wear. In M.N.H.N. no. 1903-3-9, the enamel is complete all the way around the crown, although it would be interrupted at the anterior and posterior buccal corners after very little additional wear. In the next least-worn tooth (M.N.H.N. no. 1903-3-10, Fig. 8 C), which only shows a single fossette (the mesofossette) in the posterior lobe, the enamel is interrupted antero-buccally and posteriorly, as is the case with most of the other teeth. The pattern shown in Figure 8D (M.N.H.N. no. 1903-3-11) is quickly attained, and persists indefinitely as far as can be told from the available material.

Of the three specimens believed to be M^3, two are complete and one is broken. All three, however, show a characteristic three-lobed pattern, the posterior lobe being smaller than in *Perimys*. One tooth (M.N.H.N. no. 1903-3-12, Fig. 8E) is relatively little worn. In this specimen, the enamel is interrupted at the antero-buccal corner and the extreme posterior end of the tooth. The two anterior lobes are sharply angulate, and the third lobe is quite small. A small mesofossette is present. In a more worn specimen (M.N.H.N. no. 1903-3-13, Fig. 8F), the mesofossette is lost, the second lobe is larger, and the angulation of the tooth is reduced. The enamel is interrupted along the whole buccal surface of the third lobe. As far as the base of the prism, there is no further reduction of the enamel. To judge from the structure of the anterior molars, the posterior lobe is probably formed from the posterior cingulum. The differences between the teeth shown in Figures 8E and 8F are entirely due to wear.

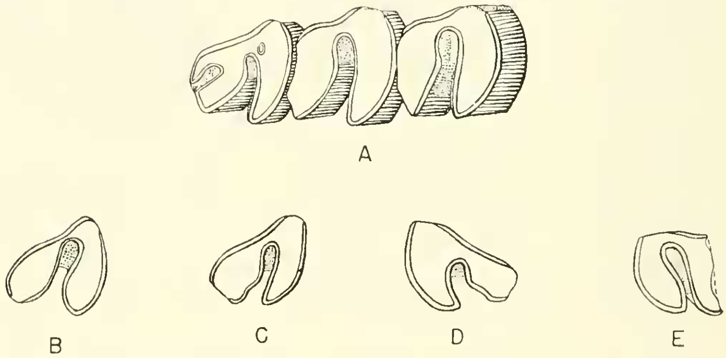

Fig. 9. *Scotamys antiquus* Loomis x 5. *A,* LP_4-M_2, type, A.C.M. no. 3063; *B,* LP_4, M.N.H.N. no. 1903-3-4; *C,* LP_4, M.N.H.N. no. 1903-3-5; *D,* RP_4, M.N.H.N. no. 1903-3-6; *E,* RM_3 (incomplete anteriorly), M.N.H.N. no. 1903-3-7. *B* to *E* show crown outlines at wear surface.

The central valley of all lower cheek teeth curves anterolinguad. At least in the stage of wear represented by most of the lower molars, each lobe is simple, all fossettids having been worn away. In unbroken lower molars, the prism may be over 7 mm. high, with no change in tooth pattern in this distance.

The least worn P_4 is that of the type. This tooth is bilobed, but there is a small antero-buccal valley in the anterior lobe and a minute fossettid, evidently a metafossettid, postero-linguad of the head of the central buccal valley (Fig. 9A). The metafossettid, however, has almost been eliminated by wear, and the anterior valley would be converted to a fossettid by a very slight additional amount of wear. This valley is directed nearly forward, partly because the protoconid has shifted forward at its buccal margin, and partly because the anterior cingulum is short at the lingual margin of the tooth. The anterior valley is filled with cement, as is the central part of the hypoflexid. This anterior valley is probably that between protoconid and anteroconid. None of the three Muséum National d'Histoire Naturelle specimens possesses an anterior valley, even as a fossettid. They apparently show a progressive transverse narrowing of the tooth with wear (Figs. 9B-D). On M.N.H.N. no. 1903-3-6, the hypoflexid ends about half way down the crown. On the lower half of the tooth, another valley appears buccally, as well as one on the lingual side, so that the pulp end of this tooth shows a figure-eight outline. This is the most worn lower premolar available. In the area with the figure-eight outline, the enamel was not laid down on the anterior face or on most of the lingual face, being present on the latter side only in the lingual valley.

In addition to those of the type, there are nine first or second lower molars in the M.N.H.N. collection. These all agree in pattern with those of the type (Fig. 9A), showing the enamel absent along the entire anterior face of the tooth and at the posterointernal corner. The central part of the hypoflexid is filled with cement, which extends part way along the sides of the flexid. Cement is also present on the posterolateral corners of the teeth. There is little or no change in pattern in the molars once the stage shown in Figure 9A has been reached. Although no unworn lower molars are preserved, there is no reason to suppose that the pattern of the lower molars was not a mirror image of that of the uppers.

M_3 (M.N.H.N. no. 1903-3-7, Fig. 9E) is similar to the anterior molars except that the talonid is appreciably narrower than the trigonid, at least at the wear surface. The difference is much less marked after further wear. The tooth is the smallest of the lower cheek teeth.

The crowns, particularly of the upper teeth, change in outline as wear proceeds. The internal cleft in P^4 disappears with wear, which gives the tooth an old *Cephalomys-Neoreomys* aspect, though arrived at in a different manner. The two sides of this cleft approach each other rather closely in old specimens of *Perimys* (e.g. A.M.N.H. no. 29673, Colhué-Huapí). Upper and lower molars of *Scotamys* are more ragged looking than in *Perimys*; they lack the neat, regimented appearance of the teeth of that form.

Three fragments of upper incisors are present in the Muséum National material. These are essentially identical in pattern with the lower incisors, but the anterior face is slightly more rounded and the pulp cavity is more nearly a straight slit than a dumb-bell shaped cavity (Fig. 10A). The lower incisor extends back to a point below M_2. It does not run beneath the cheek teeth, but rather medial of them, due to their excessive hypsodonty. The anterior face is slightly curved, and the enamel rather thick. The lateral face is markedly rounded. The enamel extends only a short distance onto the lateral side, and nearly as far on the median side (Fig. 10B). The pulp cavity is quite unusual, having a dumb-bell shape near the tip of the incisor, though it comes closer to the shape of the incisor itself several millimeters nearer the pulp end.

Both upper and lower incisors are stocky but very small in comparison to the size of the cheek teeth, a combination also true of *Cephalomys*. On this basis, *Scotamys* appears to have been a very poor gnawer. Coupled with the powerful masseter muscle and the hypselodont cheek teeth, this suggests an approach toward a grazing adaptation.

The mandible (Figs. 10C, D) is very massive and thick, with a broad, rather flat shelf on the ventral surface. The large mental foramen is in the ventral half of the jaw beneath the anterior end of P_4; two minute foramina are present above it. The chin is heavy and the symphyseal area large; the ventral margin forms a straight line terminating posteriorly in a strong mental process. The anterodorsal extemity of the symphysis extends upward above a line extended forward from the outer alveolar border of the cheek teeth. The pit for the genioglossal is pronounced. The masseteric crest is very strong, slopes gently downward and extends laterally for a considerable distance. On the dorsal side of the crest, within the masseteric fossa, there is a series of interrupted grooves. The cheek teeth are inclined laterally, as in all chinchillids and their open pulps are external to the incisor. The latter extended at least as far back as the end of the molar series, and the surrounding bone forms a shelf on the inner face of the ramus (Fig. 10D). Externally, the alveolar border of M_3 is broken away; the ascending ramus may have begun to arise from this region, as in other members of the family. For a member of the Chinchillidae, this is a primitive jaw. In the living forms the masseteric crest is reduced to the vanishing point; in *Perimys* this is much less salient than in *Scotamys*. The anterodorsal extremity of the symphysis extends as far upward in *Perimys* as in *Scotamys*, and nearly as much so in *Chinchilla* and *Lagidium*, but is low relative to the alveolar border of the cheek teeth in *Lagostomus*. The incisor extends back to M_3 in *Lagostomus*, to M_2 in *Chinchilla* and *Lagidium* and

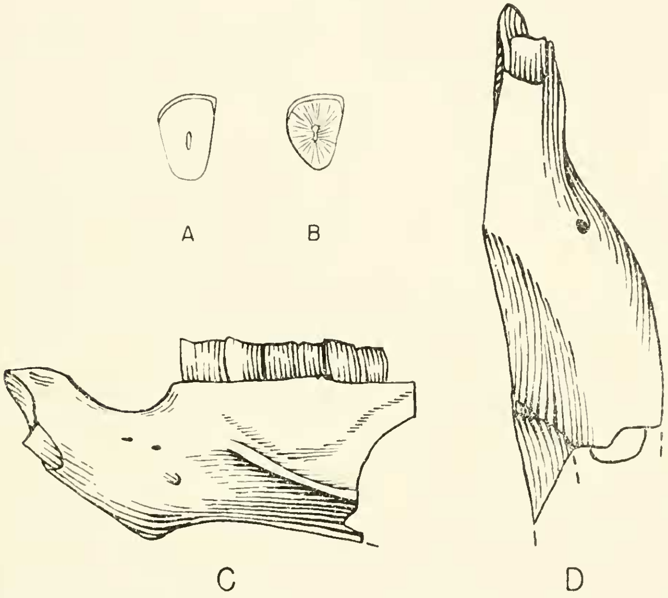

Fig. 10. *Scotamys antiquus* Loomis. Cross-sections of incisors x 5. *A*, right upper, anterior view, M.N.H.N. no. 1903-3-14; *B*, left lower of type, anterior view, A.C.M. no. 3063. Left mandible of type, A.C.M. no. 3063 x 2; *C*, lateral view; *D*, ventral view.

to varying distances in *Perimys*. The mental foramen is in the same position in *Perimys* as in *Scotamys*; much higher on the mandible in the living forms.

As regards hypselodonty, *Scotamys* is the most specialized Deseadan rodent known. Loomis (1914) placed this genus in the Chinchillidae and considered it to be ancestral to *Scotaeumys* of the Santa Cruz.[10] The upper molars of *Scotaeumys* (Scott, 1905, Pl. 68, fig. 22) could have been derived from those of *Scotamys*, but this would have involved a reversal in the direction in which the evolution of *Scotamys* had evidently been proceeding. Scott states that in P_4 of *Scotaeumys* (the only lower tooth known) there is an anterior third lamina. However, he indicates a distinct change in pattern of the upper molars with wear. From this, it would appear that *Scotamys* is appreciably more advanced in its hypsodonty than is *Scotaeumys*. *Scotamys* is therefore probably too specialized in its own direction to be ancestral to *Scotaeumys*. On the other hand, *Perimys* could have descended from *Scotamys* if the posterior cingulum of M^{1-2} were eliminated and the incisor shortened. P^4 of *Perimys* could be derived from that of *Scotamys* by an emphasis of the separation between the paracone and the anteroloph. This latter would result in the reversal of the drainage of the valley, and the formation of a buccal, rather than a lingual, cleft in partly worn teeth. In P_4, elimination of the anterior cleft, not a persistent feature in *Scotamys*, would give a *Perimys*-like pattern. *Scotamys*, then, could be a collateral ancestor of *Scotaeumys* of the Santa Cruz, and perhaps, but probably not, an actual ancestor of *Perimys* of the Colhué-Huapí and Santa Cruz. *Prolagostomus* and *Pliolagostomus* are at present of unknown ancestry, although descent from *Scotamys*, or from a form generally similar to it, is not impossible. The relationships, then, might be as shown in Figure 11.

Landry (1957a, p. 59) refers *Scotamys* to the "Cephalomyidae," although from his text (*op. cit.*, p. 54) it is obvious that he feels there are suggestions of relationship to *Perimys*. We do not differ greatly from him on this point, but we feel that the

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[10] Landry's account of the taxonomic history of *Scotamys* (1957a, p. 54) is somewhat confused. He states that it was considered to be a cephalomyid by Ameghino and Loomis. However, Ameghino had died before the genus was described, and Loomis, as stated, referred it to the Chinchillidae.

similarities to *Perimys* are indicative of phylogenetic relationships, and that the similarities to *Cephalomys* are indicative of the close approach of the two distinct lines in the Deseadan. Landry, combatting an early idea of Ameghino's that *Perimys* was directly ancestral to *Lagostomus*, has also separated some of the earlier chinchillids as a family, the Perimyidae, on the following grounds: cheek teeth with less appressed laminae, and with folds opening lingually on upper molars and labially on upper premolars; ventral maxillary zygomatic root not anterior to dorsal maxillary zygomatic root; masseteric ridge on mandible strongly developed (*op. cit.*, p. 59). As regards these characters, we may observe: 1), that *Scotamys,* which on other grounds

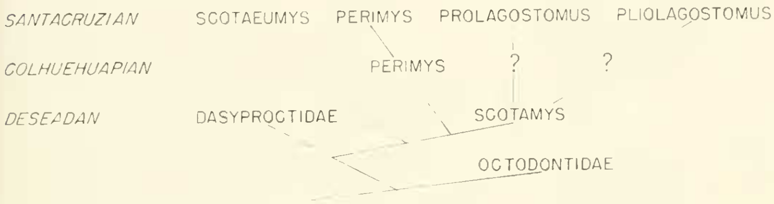

Fig. 11. Tentative phylogeny of the Oligocene and early Miocene Chinchillidae.

would be a "perimyid," has the fold in the upper premolar opening in the same direction as in the molars; and 2), that the ventral maxillary zygomatic root is just as far anterior to the dorsal root (the upper portion of the preorbital bar) in *Perimys* as it is in the living forms (Scott, 1905, Pl. 68, fig. 4, and original specimens). We are thus left with the more open folds and the masseteric ridge as the characters of the new family. As noted above, the masseteric ridge, or crest, is considerably less prominent in *Perimys* than in *Scotamys,* which suggests it was undergoing reduction through time. The folds in the upper cheek teeth of *Prolagostomus*, which Landry places in the Chinchillidae, are not as tightly appressed as in the living forms. It would seem that narrowing of the flexi and flexids was progressive in the family. *Perimys* may well have been, in these respects, a persistently primitive form, and may prove referable to a distinct subfamily when the phylogeny is better known, but we do not think that recognition of a family Perimyidae is at present helpful.

TABLE 2

Tooth measurements (in mm.) of *Scotamys antiquus*

UPPER TEETH

		M.N.H.N. No. 1903-3-8 left	M.N.H.N. No. 1903-3-47 right
P^4	anteroposterior	2.53*	2.70*
	width anteroloph	2.57*	2.21*
	width posterior lobe	1.73*	1.64*

		M.N.H.N. No. 1903-3-9 left	M.N.H.N. No. 1903-3-10 left	M.N.H.N. No. 1903-3-11 left
$M^{1 \text{ or } 2}$	anteroposterior	2.58*	2.49*	2.20*
	width protoloph	2.33*	2.41*	2.53*
	width metaloph	2.15*	2.18*	2.41*

		M.N.H.N. No. 1903-3-12 right	M.N.H.N. No. 1903-3-13 left
M^3	anteroposterior	2.84*	2.68*
	width protoloph	2.12*	2.61*
	width metaloph	2.23*	2.38*

		M.N.H.N. No. 1903-3-72 left	M.N.H.N. No. 1903-3-71 left	M.N.H.N. No. 1903-3-14 right
I^1	anteroposterior	2.19	2.07	2.25
	transverse	1.40	1.60	1.48

LOWER TEETH

		Type A.C.M. No. 3063 left	M.N.H.N. No. 1903-3-4 left	M.N.H.N. No. 1903-3-5 left	M.N.H.N. No. 1903-3-6 right
P_4	anteroposterior	2.62	2.68*	2.45*	2.97*
	width metalophid	1.74	1.75*	1.86*	1.41*
	width hypolophid	2.75	2.58*	2.38*	2.29*

			M.N.H.N., various specimens, M_1 and M_2						
			left				right		
			No. 1903-3-66	No. 1903-3-68	No. 1903-3-67	No. 1903-3-65	No. 1903-3-62	No. 1903-3-63	No. 1903-3-64
M_1	anteroposterior	2.64	2.77*	2.49*	2.15*	2.76*	2.53*	2.25*	2.23*
	width metalophid	2.38	2.48*	2.57*	2.40*	2.56*	2.63*	2.48*	2.43*
	width hypolophid	3.08	2.45*	2.56*	2.52*	2.73*	2.99*	2.73*	2.74*
M_2	anteroposterior	2.78							
	width metalophid	2.62							
	width hypolophid	2.85							

		M.N.H.N. No. 1903-3-7 right
M_3	anteroposterior	2.09*
	width metalophid	2.20*
	width hypolophid	2.08*

		Type A.C.M. No. 3063	M.N.H.N. No. 1903-3-80	M.N.H.N. No. 1903-3-79
I_1	anteroposterior	1.98	1.98	1.90
	transverse	1.52	1.50	1.51

* = Maximum diameter of tooth.

Family DASYPROCTIDAE Smith 1842

Cephalomyidae Ameghino 1897.

Two previously described Deseadan genera are here referred to this family, *Cephalomys* Ameghino and *Litodontomys* Loomis, and there is a third unnamed form that appears to belong with them. There has been much uncertainty concerning the position of *Cephalomys* and a reëvaluation of its affinities leads to certain changes in the content of superfamilies, not only as envisaged by others (e.g. Simpson, 1945) but also as envisaged by ourselves at the stage of this investigation reported by Wood (1955).

Ameghino, in establishing the family Cephalomyidae, stated that "On ne peut les placer dans aucune des familles connues de preference aux autres . . . Ils présentent un assemblage de caractères propre aux *Eriomyidae* [=Chinchillidae], *Caviidae*, *Echinomyidae* [=Echimyidae], *Hystricidae*, etc." (1897c, p. 494). At that time and subsequently, Ameghino regarded them as the basal stock for the Hystricomorpha (*sensu lato*). Loomis (1914, p. 186) put *Cephalomys* in the Chinchillidae, as ancestral to *Perimys* of the Santa Cruz.[11] Miller and Gidley (1918, p. 445) placed *Cephalomys* and *Litodontomys* in their subfamily Octodontinae (our Octodontidae plus Ctenomyidae) of the family Echimyidae. L. Kraglievich (1940a, p. 441) considered the Cephalomyidae to have been ancestral to the Eocardiidae and, through them, to the Caviidae and Hydrochoeridae. Simpson's

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[11] Landry (1957a, p. 54) states that Ameghino and Loomis placed *Cephalomys* in the Caviidae and that Simpson referred it to the Chinchillidae. However, Ameghino never considered it as anything but the type of his family Cephalomyidae, Loomis referred it to the Chinchillidae, and Simpson accepted Ameghino's Cephalomyidae.

classification (1945, p. 94) placed them in a similar position. We formerly referred them to the Capromyidae (*in* Wood, 1955). Landry (1957a, pp. 54 and 59), considers the Cephalomyidae to be a basal family of the Chinchilloidea, from which he excludes *Dasyprocta*. It appears to us that almost every allocation except the right one, or so we now think, has been made.

There are no very striking resemblances between *Cephalomys* and the Cavioidea in general, or the Eocardiidae in particular, other than those common to most of the South American rodents. Some similarities exist in the general outlines of worn teeth, but the details of the tooth structure of *Cephalomys* are very different from those of *Eocardia* (cf. figures given here with those in Scott, 1905, Pl. 69). The resemblance to *Perimys,* pointed out by Loomis and by Landry, is definite, but again is most prominent in worn teeth, and is largely confined to the upper molars. The reversal of pattern between worn upper premolars and molars is present in both of these genera, however, and this is of interest and is discussed below. The cheek teeth are far more advanced than those of the contemporary octodontids and echimyids. Now that unworn teeth are available, it has become apparent, as pointed out below, that there is great similarity, although not identity, in the dentition between *Cephalomys* and *Neoreomys* of the Santa Cruz, which we think indicative of affinity, and this is supported by what is known of skull structure. Since Scott's study (1905) of the Santacruzian rodents, the view that *Neoreomys* and apparently related genera — *Scleromys* and *Olenopsis* — were capromyids or myocastorids has been rather generally held. Accepting this, without more ado we considered *Cephalomys* and, tentatively, *Litodontomys* to be capromyids. Further, noting the close resemblance in cheek tooth structure between *Cephalomys* and the contemporary chinchillid *Scotamys* Loomis, we transferred the Capromyidae from the Octodontoidea of Simpson's classification to the Chinchilloidea (Wood, 1955). It would now appear that our acceptance of *Neoreomys* as a capromyid and the allocations based on this acceptance were in error.

We had noted the replacement of dm_4^4 by P_4^4 in *Neoreomys,* a difference from the Capromyidae, in which, as in post-Deseadan Echimyidae, there is no such replacement, but had supposed that retention of the milk teeth in the family had come about in post-

Santacruzian time.[12] However, reinforcing this difference, there is also a cranial character that sets *Neoreomys* sharply apart from the Capromyidae. In the latter group there is a process from the supraoccipital (the lateral process of Tullberg, 1899, p. 69) that projects downward parallel and anterolateral to the paroccipital process, from which it is separated by a narrow notch. This process is very large in *Myocastor* and of more modest dimensions in the other capromyids. It also occurs in echimyids, ranging in size from incipient to small, and in erethizontids. The structural base for such a process is present in Santacruzian (*Sciamys,* Scott, 1905, Pl. 67, fig. 9) and Recent octodontids, and in abrocomids and ctenomyids, in which a strip from the supraoccipital extends down to a point above the attachment for the stylohyal but does not form a process. In the Deseadan *Platypittamys,* however, so far as can be determined from the crushed material, there is not even a rudiment of such a strip. This suggests that the strip — and the process that could arise from it — was not a part of the original caviomorph heritage but arose independently more than once. The primitive octodontids could have given rise to groups with and without this character, and the possibility of its later rise in other groups cannot be excluded. Landry (1957a, pp. 74-75) correctly points out that this feature is widespread and sporadic among rodents. In one very young specimen of *Erethizon* seen by us the "process" starts as an independent ossification, separate from the supraoccipital. The complete absence in *Neoreomys* of even the rudiment of a supraoccipital strip (see Scott, 1905, Pl. 54, figs. 6, 6c), not to mention a lateral process, coupled with replacement of dm_4^4, however, would appear to exclude this form from the Capromyidae. The latter family, as probable echimyid derivatives, should be returned to the superfamily Octodontoidea.[13] The combination of lateral process and unreplaced dm_4^4 so neatly reinforces other characters that suggest a close relationship between the Echimyidae and the Capromyidae that it is almost a pity to have to introduce a note of caution.

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[12] The supposedly Santacruzian *Paramyocastor* Ameghino (1904) is actually from the Pliocene Hermosan (J. L. Kraglievich, personal communication).

[13] We are greatly indebted to Drs. Ernest E. Williams, Karl Koopman and Samuel B. McDowell for their kindness in pointing out to us the important lack of a lateral process in *Neoreomys*.

Rodents being what they are, however, we are compelled to observe that the two characters do not always go together in the Caviomorpha. *Elasmodontomys* has a lateral process second only to *Myocastor* in point of size, yet its milk molars are shed,[14] a feature that scarcely admits it to either the Capromyidae or the Echimyidae.

Neoreomys and *Cephalomys* being excluded from the Capromyidae, the question of their familial position comes to the fore. Fortunately we do not have far to seek for an answer, no farther in fact that the work of Scott, who (1905, pp. 387-399) very clearly pointed out the many resemblances of *Neoreomys* to *Dasyprocta* and *Cuniculus*. Quite obviously, he felt that *Neoreomys* could almost equally as well be referred to the Dasyproctidae as to the Capromyidae. Following the hint contained in his work, and in agreement with Miller and Gidley (1918, p. 447) and Winge (1924, pp. 66, 77), we now refer *Neoreomys* and its relatives to the Dasyproctidae.

Scott's work, moreover, contains a further hint of interest in this connection: ". . . . the likenesses of *Neoreomys* to the *Dasyproctidae* and *Dinomyidae* are also very suggestive and indicate that this genus is not far removed in structure from some earlier and more generalized form, which was the common ancestral stock of several distinct families" (1905, p. 387). We are in complete agreement with Scott that *Neoreomys* suggests some degree of relationship between Dasyproctidae, Cuniculidae and Dinomyidae. With Schaub (*in* Stehlin and Schaub, 1951, pp. 369-370), and Landry (1957a, pp. 44, 57-58), we now believe that these families should be removed from the Cavioidea of Simpson's classification, thus limiting that superfamily to the Eocardiidae, Caviidae and Hydrochoeridae. We agree with Schaub that the Cuniculidae and Dinomyidae should be associated with the Chinchillidae, and to these we would add the Dasyproctidae, which he left as *incertae sedis* together with the "Cephalomyidae" (Schaub, 1953a, pp. 396-397). The West Indian *Elasmodontomys* group may also be included here, at least

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[14] *"Heptaxodon"* is in fact based on young individuals of *Elasmodontomys* with dm $\frac{4}{4}$. The fine material now available, much of it obtained since Anthony's work on these forms, includes enough of the growth stages to relieve all doubt on this head. This question will be discussed in a forthcoming study of West Indian rodents by Mr. Clayton E. Ray.

provisionally. For this assemblage the earliest available name is Chinchilloidea L. Kraglievich 1940. We agree with Schaub, Stirton (1947), Landry (1957a) and Fields (1957) that the extinct Eumegamyinae belong in the Dinomyidae and not in the *Elasmodontomys* group.

Landry (1957a, pp. 57-59) groups the Myocastoridae (including *Neoreomys*), Cuniculidae (including *Dasyprocta*), Dinomyidae, Octodontidae and the *Elasmodontomys* group in the Octodontoidea. As we have indicated, we consider *Neoreomys* to be a dasyproctid. *Eumysops*, which Landry refers to the Myocastoridae,[15] is an echimyid. We feel that the distinction between the Cuniculidae and Dasyproctidae is sufficient to justify their familial separation, and that, as we have just indicated, they should be referred to the Chinchilloidea, while *Myocastor* surely belongs with the Echimyidae and Capromyidae in the Octodontoidea. The Chinchillidae, as represented by *Scotamys,* and the Dasyproctidae, as represented by *Cephalomys,* are very similar in most details of crown structure in the Deseadan. Both forms have molars in which the structural details are rather shallow, in the former somewhat shallower than in the latter. This, we suspect, foreshadows a marked difference between later representatives of these two rapidly diverging families. In the Dasyproctidae, the evolutionary trend was toward the preservation and increase of crown complexity, the crown growing down toward the root, as it were. Chinchillid molar evolution proceeded in almost precisely the opposite direction, eliminating all the minor features of the cheek tooth crown, deepening only the clefts between the lobes.

Cephalomys, in view of its resemblance to *Neoreomys* and to the contemporary chinchillid *Scotamys,* seems surely to be a member of this group, but its exact position within the superfamily is uncertain. As is emphasized below, the upper molars of *Neoreomys* and *Cephalomys* are not identical; they differ in the structure of the neoloph and in the extent of enamel deposition. There are also differences in the skull and mandible, which are generally, but not entirely, due to *Cephalomys* being the more primitive. Although the two forms are, we believe, related,

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[15] A deduction from the position occupied by the genus in L. Kraglievich's list (1934, p. 30) of Argentinian Pliocene rodents (Landry, pers. comm.).

they are most certainly not ancestor and descendant. In fact, *Cephalomys* cannot at present be brought into direct relationship with any later rodents, which is rather curious in view of its great abundance in the Deseadan. For the moment it can only be regarded as representing a very successful although short-lived phylum. *Litodontomys* may be related to the type species of *Olenopsis* although this is uncertain. The third Deseadan form, represented only by an isolated upper cheek tooth in the Ameghino Collection, was, on this slender evidence, perhaps close to the Santacruzian *Scleromys,* and may conceivably, therefore, have something to do with the ancestry of this form. The only known Colhué-Huapí form possibly referable to the Dasyproctidae is represented by an isolated upper molar intermediate in some respects between those of *Neoreomys* and *Scleromys.* Divergence was clearly under way during the Deseadan, but presumably had not begun very long previously. The phylogeny of these forms was certainly complex. We undoubtedly know only a small fraction of the forms that once existed.

It will be evident that in a situation such as this taxonomic assignments can only be tentative. There is no available evidence that any of the Santacruzian and earlier forms are members of the Cuniculidae. There is a possibility that some of them may be dinomyids. Very recently, Fields (1957) has published a valuable paper on late Miocene rodents, especially Dinomyidae, from Colombia. He refers the species of this family represented among his material to *Scleromys* (in which he includes *Lomomys*) and to *Olenopsis*, the type species of which are Santacruzian. There is no question as to the familial position of the Colombian species, but we feel some uncertainty as to the generic references. As pointed out below under *Litodontomys*, there is doubt as to whether the Santacruzian species of *Olenopsis* is congeneric with the Colombian one described by Fields. We reserve judgment, pending further knowledge of the type species of both genera. The Colhuehuapian material (including Stirton's 1953, p. 611, record of teeth of *Scleromys*? from Colombia) is so fragmentary as to permit no certainty as to familial position. Continued recognition of the family Cephalomyidae for the reception, primarily, of one seemingly aberrant genus is hardly warranted. Our present, very tentative, conception of affinities within this very complex and little understood group is shown in Figure 12.

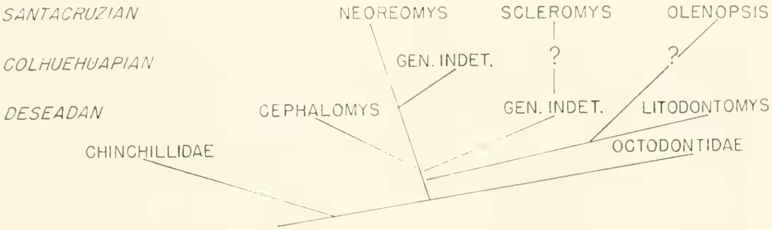

Fig. 12. Tentative phylogeny of the Oligocene and early Miocene Dasyproctidae.

CEPHALOMYS Ameghino, 1897

Cephalomys Ameghino 1897c, p. 494. Loomis 1914, pp. 186-188; Stehlin and Schaub 1951, p. 61; Schaub, *in* Stehlin and Schaub 1951, pp. 245-246.
Orchiomys Ameghino 1897c, p. 495.
Asteromys Ameghino 1897c, p. 495; 1902b, p. 37 (in part, not including type species).

Type species. Cephalomys arcidens Ameghino 1897.

Referred species. Cephalomys plexus Ameghino 1897.

Type species of synonym. Orchiomys prostans Ameghino 1897.

Distribution. Deseadan, Patagonia.

Emended diagnosis. Teeth high-crowned but rooted, with unilateral hypsodonty, particularly in upper molars; no cement on crowns; crown pattern of unworn cheek teeth essentially resembling that of *Neoreomys*, also basically similar to that of *Platypittamys* but with P_4^4 much more advanced than in latter; pattern disappearing fairly rapidly with wear, much less persistent than in *Neoreomys;* enamel interrupted on lingual and anterior sides of lower teeth and buccal and posterior sides of upper teeth after considerable wear; rostrum shorter than in *Platypittamys,* narrower than in *Neoreomys*; fossa for M. massetericus medius pars anticus present on lateral surface of rostrum but smaller than in *Neoreomys*; infraorbital foramen very large, larger than in *Neoreomys*; mandibular condyle low, nearly on level of cheek teeth.

The synonymy is discussed below under the species.

DENTITION

All the cheek teeth of this genus are divided into two lobes. In the upper molars, these lobes unite, after wear, on the buccal side of the crown; in the lowers, at the center of the tooth. The molars are made up of five cross crests above and four below, but the valleys between the members of the anterior and posterior sets of crests are shallow and evanescent.

Several specimens in the Amherst, Buenos Aires, Chicago and Paris collections show unworn or essentially unworn cheek teeth, from which the details of the pattern can be determined for nearly all of the teeth.

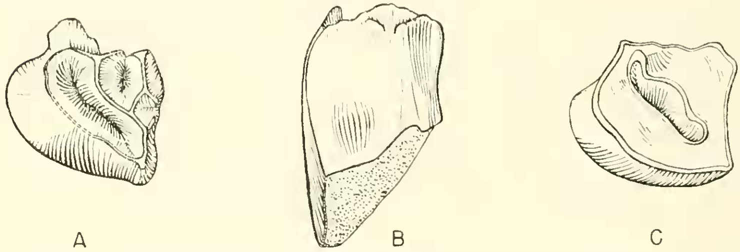

Fig. 13. *Cephalomys arcidens* Ameghino, LP^4 x 5. *A* and *B*, crown and posterior views of A.C.M. no. 3122; *C*, crown view of A.C.M. no. 3064.

Two unworn and two little worn P^4 are available: A.C.M. no. 3122 (Fig. 13A and B), C.N.H.M. nos. P15241 and P14652 (Fig. 14A) and M.N.H.N. no. 1903-3-23. These agree closely in essentials. There is a long narrow blade extending across the anterior and lingual sides of the crown to unite posterointernally with the straight, transverse posterior margin of the tooth. In the middle of the buccal side is a large cusp that sends a curved crest posterad to the posterior margin. A little distance anterior to the point of junction, a short oblique ridge runs anteroexternally between this crest and the posterior margin, isolating a shallow, posteromedian fossette on three of the teeth. The interpretation of this structure seems clear. The large, curving anterior and internal crest is certainly the anteroloph plus protocone; the large buccal cusp is the paracone; and the crest curving posteriorly from it is a protoloph that has lost contact with the protocone. The transverse, posterior crest may be interpreted as the posteroloph with the metacone incorporated in its external portion, precisely as in *Platypittamys* and *Deseadomys.* The short, oblique crest connecting the posteroloph and the protoloph appears to be the serial equivalent of the corresponding additional crest (neoloph) of the molars (see below) rather than a metaloph. A hypocone, as such, is not differentiated and there is no trace of a hypoflexus. P^4 of the contemporary chinchillid *Scotamys,* which is a basically similar tooth, has a very shallow hypoflexus. This suggests that the hypocone may have been slightly differentiated, or that a tendency existed toward its differentiation, in the common ancestry, perhaps to the extent seen in *Platypittamys.* The Santacruzian *Scleromys,* which has a deep hypoflexus and a well defined hypocone in P^4, also suggests that this was the case and that, furthermore, divergence took place among these forms, *Cephalomys* and *Neoreomys* obliterating, the Santacruzian *Scleromys* accentuating the hypoflexus. According to Fields' figures (1957), the Colombian species he refers to *Scleromys* agree in this respect with *Cephalomys* and *Neoreomys.* However, his figures indicate that P^4 in his forms is more molariform than in *Cephalomys.*

Minor variations in pattern occur in all specimens. In M.N.H.N. no. 1903-3-23, which is very slightly worn, there are irregularities in the buccal margin of the paracone, not indicated in the other specimens. The paracone of the unworn C.N.H.M. no. P15241 is broad and quadrilateral, instead of being a thin blade. There is a clearly marked depression on its top, surrounded by ridges of thick enamel and floored with a thin veneer of enamel. There are three buttresses of enamel running down the buccal margin of the cusp, which would give its outer border a fluted pattern if the tooth were slightly worn. There are two small knobs on the posterior face of A.C.M. no. 3122. These differences in the details of the crown (seen also in the unworn molars) are not considered to have any taxonomic significance. Variation of this sort (which would be considered of specific or even generic value in brachyodont teeth) is a very common feature in the portions of the crown pattern of extremely hypsodont teeth that have not taken part in the increased hypsodonty, and is of no taxonomic significance whatever (Wood, 1940, p. 300), though it may give clues to the phylogeny of the animals concerned.

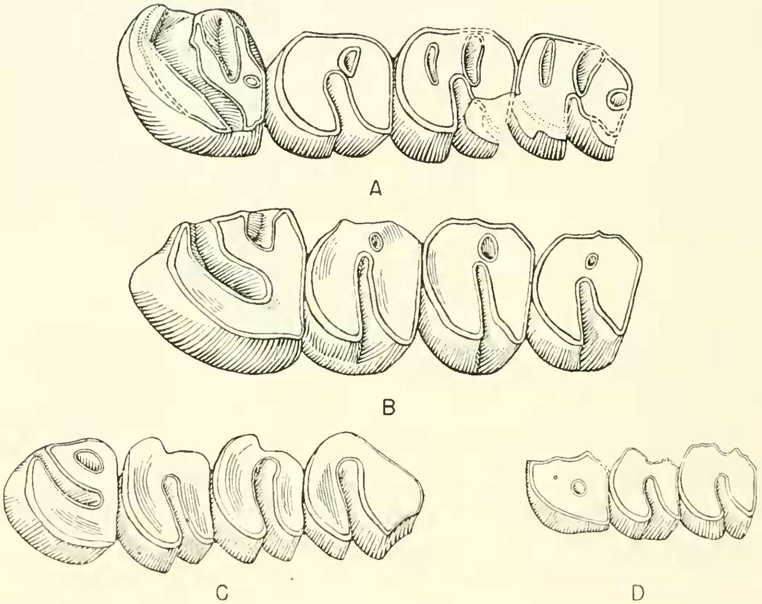

Fig. 14. *Cephalomys,* upper cheek teeth, x 5. *Cephalomys arcidens* Ameghino. *A,* LP^4-M^3, C.N.H.M. no. P 14652; *B,* LP^4-M^3, A.C.M. no. 3099 (M^3 reversed from right side of same specimen). *Cephalomys* sp. *C,* LP^4-M^3, A.C.M. no. 3109. *Cephalomys plexus* Ameghino. *D,* LP^4-M^2, A.C.M. no. 3085.

The first development during wear of P^4 is the isolation of a small lake between the knobs on the posterior surface, when these are present (Fig. 14A). Further wear produces a trident-like pattern (Fig. 14B), and then eliminates all the pattern except for the valley behind the protocone-anteroloph blade, which remains as a lake reaching almost to the roots (Fig. 13C). The sequence of pattern changes with wear (at least in *C. arcidens*) is as follows:

1. elimination of minor irregularities and formation of posterior lake (Fig. 14A);
2. elimination of posterior lake and development of trident pattern (Fig. 14B);
3. conversion of posterior external valley to a lake (Fig. 14C);
4. elimination of posterior external lake (Fig. 13C);
5. conversion of anterior valley to a lake (Fig. 13C);
6. interruption of enamel on posterior face.

In *Cephalomys plexus*, it seems that there may be variability in the sequence, with some specimens agreeing with that listed above (Fig. 14D), whereas in others stage 6 precedes stages 4 and 5 (Fig. 22B), as is also true in *Cephalomys* sp. (Fig. 14C).

The upper premolars of the dasyproctid *Cephalomys* and of the chinchillid *Scotamys* are very similar, differing only in that the latter apparently lacks a neoloph, and has an internal opening of the paraflexus. Superficially, they appear to be quite different from those of the early octodontids, yet closer inspection reveals that all the ingredients for them are represented in P^4 of *Platypittamys* and *Deseadomys*. To convert premolars of this type into the *Cephalomys-Scotamys* P^4 would require only the posterior growth of the protocone, loss of contact between the paracone and the protocone, and a posterior shifting of the lingual end of the paracone crest as the protocone shifted to the rear. This paracone shift might have been facilitated by capture of an incipient mure of the type seen in *Deseadomys* (Fig. 4).

An entirely unworn left upper molar (probably M^3) of *C. plexus*, M.N.H.N. no. 1903-3-3, reveals every detail of the crown (Fig. 15A). Four crests are present, the third crest running obliquely to the posteroloph in the more buccal part of its course. This crest we take to be the lingual part of the metaloph plus a diagonal neoloph crossing the metaflexus. The protoloph, lingual part of the metaloph, neoloph and the buccal part of the posteroloph are the highest parts of the crown, and are practically at the same level, the anteroloph being slightly lower, especially buccally. The lingual portion of the posteroloph is considerably lower and is bowed posteriorly at the occlusal surface, though not at a lower level of the crown. At the posteroexternal angle of the tooth, and somewhat below the level of the rest of the crown, is a small cuspule, from which a short crestlet runs antero-lingually. By comparison of this tooth with the slightly worn first or second upper molars of *C. arcidens* shown in Figures 15B and C, this cusp would appear to be the metacone, and the crestlet running from it to be the last stage in the degeneration of the buccal part of the metaloph. In the specimens shown in Figures 15B and C, the metaloph is complete and five crests are present. This may be a specific character, but is probably an individual variant, since, in upper molars of *Neoreomys australis* (Fig. 17A), and especially in M^3, the metaloph exhibits various stages of disintegration. The neoloph in *Cephalomys* has split the metafossette into two parts, the posterior one (which may be termed the lingual neofossette) being large, irregularly trumpet-shaped, but decreasing rapidly in size with depth. Only a moderate degree of wear would eliminate both parts of the metafossette entirely, and no suggestion of the presence of the neoloph would remain. The parts of the metafossette are worn away in all other available material except C.N.H.M. no. P14652, where the lingual neofossette is preserved on M^3 (Fig. 14A).

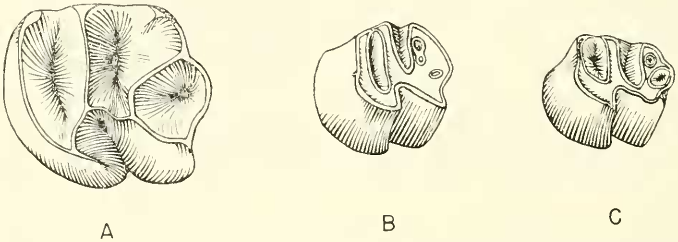

Fig. 15. *Cephalomys*, unworn and little worn upper molars. *Cephalomys plexus* Ameghino. *A*, LM^3, M.N.H.N. no. 1903-3-3, x 10. *Cephalomys arcidens* Ameghino. $LM^{1 \text{ or } 2}$, x 5; *B*, M.N.H.N. no. 1903-3-22; *C*, M.N.H.N. no. 1903-3-20.

This peculiar development of a diagonal neoloph directed anterointernally might at first glance seem to separate *Cephalomys* widely from all other caviomorphs. However, investigation of unworn teeth of various members of the suborder shows that it is by no means a unique feature, appearing in several forms as an individual variation. For example, it is also present in some specimens of *Erethizon dorsatum epixanthum* (Fig. 1D). In *Coendou brandti* we have seen the neoloph extending to the hypocone. Landry figures an interesting case in *Dasyprocta fuliginosa* (1957a, Pl. 5, fig. a) in which the neoloph seems to have split into two parts, one diagonal and one transverse, and we have seen the same thing in *D. aguti.* Evidently this part of the upper molars of caviomorphs is quite unstable.

The angulations at the ends of the neoloph on M.N.H.N. no. 1903-3-3 would be eliminated by wear about the same time the lingual neofossette was lost (Fig. 15A). The great depths of the hypoflexus, mesoflexus and paraflexus are strikingly apparent, the hypoflexus being the deepest, followed by the mesoflexus and paraflexus in that order. The anteroloph and protoloph unite at the buccal margin of the tooth a short distance below the apex of the crown so that the parafossette is isolated soon after wear begins. The protoloph and metaloph (or its vestige) unite considerably farther down, the mesofossette becoming isolated about the time the lingual neofossette disappears (cf. A.M.N.H. no. 29558 or C.N.H.M. no. P14652, Fig. 14A), or later (Fig. 16A). The mure is slightly angulate, but shows no thickening that would suggest the presence of a mesocone.

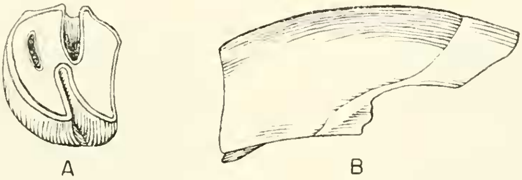

Fig. 16. *Cephalomys arcidens* Ameghino. A.C.M. no. 3160, LM$^{1\text{ or }2}$, x 5; *A*, crown, and *B*, anterior views.

In addition to giving us the crown pattern of an upper molar of a member of this genus, these teeth are interesting because of the similarity — apart from the neoloph — to the unworn molars of *Neoreomys* (Fig. 17A). In the latter, there is also a fifth crest, but this seems to be a normal neoloph, a development from the posterolophid, as in *Protosteiromys*, since it is connected at both ends with that crest, and has no connections whatever with the hypocone. There is a good metacone in *Neoreomys,* which is sometimes partially isolated from the lingual part of the metaloph as in *Cephalomys,* and which thus looks like part of a mesoloph, which it certainly is not. This difference between the manner of development of the fifth crest in *Cephalomys* and *Neoreomys* merely emphasizes the great plasticity of rodent cheek tooth patterns, and the fact that variants may (and generally do) arise in a wide variety of different manners. Perhaps this discrimination of minor types of neoloph variation may seem to be ultrafastidious but one of the difficulties in unraveling rodent evolution has been the tendency to overlook such differences in origin of a pattern, or to assume that these differences are of no phylogenetic significance. The development of a neoloph, of various types, seems to be characteristic of the caviomorphs, and to distinguish them from the hystricomorphs, where the fifth crest appears to be a mesoloph.

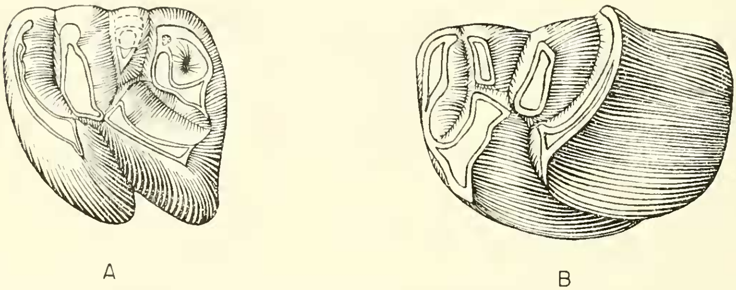

Fig. 17. *Neoreomys australis* Ameghino. C.N.H.M. no. P 13164, x 5; *A,* LM^2; *B,* LM$_2$.

The primary difference in pattern between the premolars and the molars is that, in the latter, the hypocone is a large and independent element, which it is not in the premolar. This presumably means that the teeth represent specializations of something like those of *Platypittamys,* and that, in the premolar, the protocone grew backward along the lingual margin of the tooth, taking over the functions of both protocone and hypocone in the molars. An additional difference is that the main valley of the premolar is deeper buccally than lingually, so that, with wear, it opens on the buccal side of the tooth, as in chinchillids.

With wear, the molars pass through the following stages:

1. crown formed of anteroloph, protoloph, metaloph or remnant, posteroloph and neoloph, the last dividing the metafossette into two parts (Figs. 15B-C);
2. paraflexus converted to a parafossette (Fig. 14A);
3. elimination of all parts of metafossette;
4. mesoflexus converted to mesofossette (Fig. 14A);
5. elimination of parafossette (Fig. 14B);
6. interruption of enamel on buccal surface (Fig. 14B);
7. elimination of mesofossette;
8. interruption of enamel on posterior surface (Fig. 14C).

Fig. 18. *Cephalomys arcidens* Ameghino. RP$_4$ x 5. *A*, A.C.M. no. 3108; *B*, M.N.H.N. no. 1903-3-19.

The little worn lower premolar (Figs. 18A, 19A, and 19E) shows a pattern rather distinct from that of the lower molars. The trigonid consists of a metaconid, a protoconid and an anteroconid. All of these elements are exceedingly narrow and compressed on the unworn surface, showing little or no suggestion of separate cusps. The protoconid curves forward at its buccal end, and the anteroconid extends straight forward, so that, in unworn or partly worn teeth, there is an anterior lobule (Fig. 18A) giving this tooth a distinctive appearance. Various specimens show notable variation in the anteroconid, which is in part intraspecific (Figs. 18A, 18B, 19A, *C. arcidens*) and is in part associated with the fact that two distinct species are represented. In the unworn P$_4$ of *C. arcidens* the tip of the anteroconid is connected with the anterolophid, whereas in unworn *C. plexus* it stands free (A.C.M. no. 3113, Fig. 19E, and M.A.C.N. nos.

A 52-103, and A 52-106). The talonid in slightly worn teeth consists of a single lobe, connected diagonally with the middle of the metalophid. This diagonal crest arises from the central part of the talonid. Unworn teeth, however, show that the lingual margin of the talonid is actually subdivided into two crests, the hypolophid and the posterolophid. The division extends neither very far across the tooth nor very far down the crown. The entoconid is considerably higher than the posterior cingulum. The enamel over the latter is very thin, sometimes appearing almost not to have been deposited. The apparent pinching at the waist of A.C.M. no. 3108 (Fig. 18A) is due to the lower part of the crown being buried in the jaw. If this tooth were fully erupted, the outline would presumably be the same as that shown in Figures 18B and 19A. The crown pattern is so shallow and so rapidly worn away that there is really no sequence in its loss.

All three lower molars show essentially the same pattern, which may be very clearly seen in M_{1-2} of M.N.H.N. no. 1903-3-2 (Fig. 19B) and in M_3 of A.C.M. nos. 3162 and 3113 (Figs. 19C and E). This pattern is obviously the same as that of *Neorcomys* (Fig. 17B). Again there is variation among the specimens referred to the two species of the genus. The anterolophid extends across the anterior face of the tooth, reaching the lingual margin of the crown, uniting with the metaconid either at or a short distance below the level of the crown. It gives the appearance of having been prevented from growing forward by the presence of another tooth in front, whereas the absence of such a tooth permitted forward growth in the premolar. The anterofossettid is quite ephemeral, though not as short-lived as the metafossettid of P_4. The hypolophid curves slightly to the rear, swinging forward to join the metaconid a short distance below the crown surface. In the crown view of an unworn tooth, the entoconid appears to have its relationships with the trigonid rather than with the talonid (Figs. 19C, E). However, the valley between this crest and the metaconid is actually much deeper than that between it and the rest of the talonid. The latter consists of a long lobe, believed to be formed of the hypoconid and posterolophid. In *C. arcidens*, the posterolophid is incipiently subdivided near its lingual margin in one specimen (Fig. 19C), in a manner that might be the initial stage in the development of an additional lobe. The roots have not yet formed on these unworn third molars, though they probably soon would have developed since they have formed on the second molars of the same specimens.

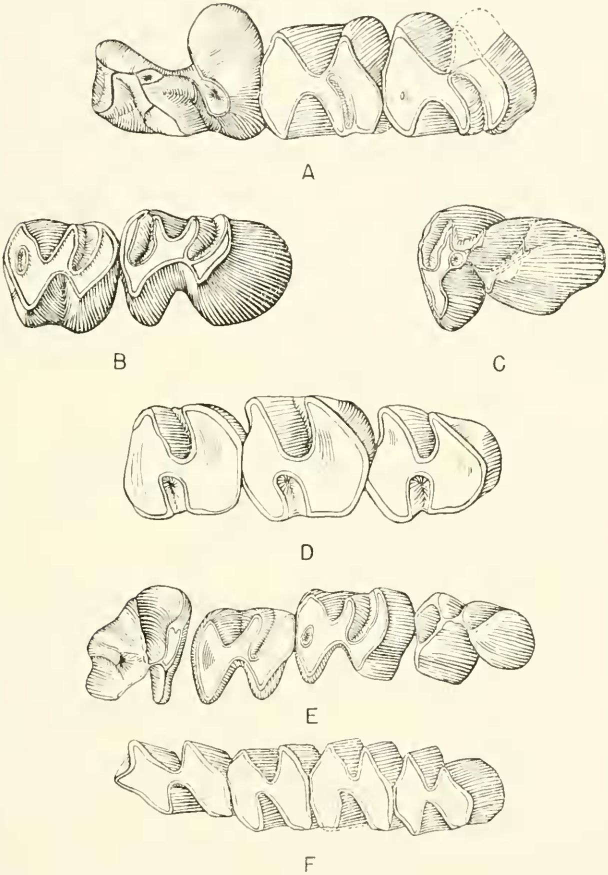

Fig. 19. *Cephalomys*, lower cheek teeth, x 5. *Cephalomys arcidens* Ameghino. *A*, RP$_4$-M$_2$, A.C.M. no. 3161; *B*, LM$_{1-2}$, M.N.H.N. no. 1903-3-2; *C*, LM$_3$, A.C.M. no. 3162; *D*, RM$_{1-3}$, A.C.M. no. 3078. *Cephalomys plexus* Ameghino. *E*, LP$_4$-M$_3$, A.C.M. no. 3113; *F*, RP$_4$-M$_3$, A.C.M. no. 3006.

In another specimen of *C. arcidens* (A.C.M. no. 3144), there is a slightly more worn M_3. In this tooth, though damaged, the metaconid and anterolophid have nearly united lingually. In *C. plexus* they may (A.C.M. no. 3113, Fig. 19E) or may not (e.g. M.A.C.N. no. A 52-103) be united lingually on unworn teeth. The entoconid is shorter, on the crown surface, in A.C.M. no. 3144 than in the previously described specimens, and the talonid is broken. The valley between the metaconid and entoconid is 5.0 mm. deep at the lingual edge of the tooth, extending within 0.6 mm. of the base of the enamel on the crown. The roots are formed in this tooth, so that the crown height can be determined to have been approximately 5.6 mm. on the lingual side and 7.5 mm. on the buccal side.

The sequence of loss of crown pattern in the lower molars is as follows:

1. wear to produce a flat surface with loss of minor irregularities;
2. conversion of the anteroflexid (in *C. arcidens*) to a lake, as in unworn *C. plexus* (Fig. 19E);
3. loss of the anterofossettid (Fig. 19A);
4. conversion of hypoflexid to a lake (Fig. 19A);
5. loss of hypofossettid;
6. interruption of enamel on anterior face (Fig. 19D);
7. conversion of mesoflexid to a lake;
8. interruption of enamel on lingual face.

This sequence of events is based on *C. arcidens*. There may be slight differences in the sequence in *C. plexus*, but they are not very significant. In general, through stage 6, each tooth is about one stage ahead of the next one behind it.

Four specimens in the Amherst and two in the Ameghino collections show dm_4. There is a certain amount of variation in the anterior part of the crown, which is not unusual among rodents (Figs. 20A, B). The talonid seems to be similar to that of the permanent teeth, except that the valley between the entoconid and the posterolophid is as deep as any other valley in the crown. The talonid is connected to the center of the straight metalophid. Anterior to this is what seems to be a tripartite anteroconid, connected to the protoconid or to the protoconid and metaconid. There are two buccal, one anterior, and four lingual valleys. The tooth is replaced after M_1 has reached wear stage

3 or 4, and M_2 wear stage 2 or 3, and very shortly after M_3 has come into use.

The crowns of all the teeth were covered by a complete enamel cap, even though it was removed very quickly by wear. That on the upper surface of the talonid of P_4 was so thin as to appear absent (Fig. 19E). Its thinness in this specimen cannot be due to wear, however, unless the wear was against the roots of dm_4, since we personally removed the roots from over this part of the crown in A.C.M. no. 3113.

The enamel extends to varying distances down the sides of different parts of the crown of the cheek teeth, due to the asymmetric development of hypsodonty. It is interrupted, after the tooth is about half worn down, along the anterior faces of the lower molars (Figs. 19D, F). Before this level is reached, the thickness of the enamel is considerably reduced by interdental wear (Fig. 19A).

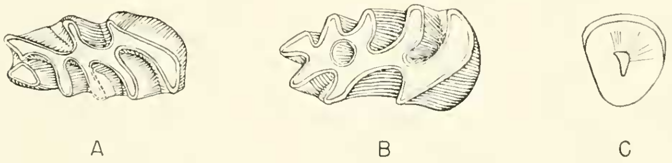

Fig. 20. *Cephalomys arcidens* Ameghino, lower teeth, x 5. *A,* Rdm_4, A.C.M. no. 3013; *B,* Ldm_4, A.C.M. no. 3011; *C,* cross-section of RI_1, anterior view, A.C.M. no. 3155.

The enamel is next lost on the posterointernal corner of the entoconid, beginning with M_1. This occurs much earlier in *C. plexus* (Fig. 19F) than in *C. arcidens.* A layer of cement is deposited around the basal portions of the crown, particularly in *C. plexus,* which sometimes makes it difficult to determine the exact points at which the interruptions occur. In the upper molars, since the teeth are high-crowned lingually and low-crowned buccally, the initial point of loss of enamel is the buccal surface of M^1, followed in turn by M^2 and M^3. The enamel is then lost on the posterior faces of the same teeth. Before the level of no enamel is reached, the buccal enamel becomes considerably thinned, which is obviously not due to interdental wear.

These interruptions are certainly primarily due to non-deposition, and not to interdental wear, as may be seen by looking at the anterior or posterior faces of slightly worn teeth (Fig. 16B), where the uneven ends of the enamel may be seen on the intra-alveolar portions of the teeth. Conditions appear to be identical with those described for the Lagomorpha (Wood, 1940, pp. 356-357). After the portion of the tooth with interrupted enamel has reached the occlusal surface, however, interdental wear becomes quite prominent, and the shapes of the teeth may change considerably and quite rapidly, due to the wear of the enamel of one tooth against the dentine of the adjacent tooth (H. E. Wood, 1938).

The crowns of the teeth are quite high, the height in unworn upper premolars and M_3 reaching twice their maximum diameter.

The difference in pattern between slightly worn lower premolars and molars is believed to be due to two factors: 1) the anterolophid of P_4 extends anterad, whereas in the molars it is squeezed parallel to the metaconid; and 2) the entoconid of P_4 is closely united with the posterolophid, on the wear surface as well as farther down the crown. However, the difference in pattern between both upper and lower premolars and the molars indicates that the molarization of the premolars in this, as well as in other Deseadan genera in which the premolars are known, occurred at a time when the molars had already acquired the main elements of their pattern, while the premolars were relatively simple. It would therefore be in accord with the derivation of *Cephalomys* from something quite similar to *Platypittamys.*

The lower incisor has a nearly flat but gently curved anterior face (Fig. 20C). The enamel face bears a series of fine lines, nearly parallel to the long axis of the tooth. The enamel extends over about a third of the lingual side and about half the buccal side of the tooth. The incisors are relatively short and narrow in proportion to the size of the cheek teeth. The pulp cavity is roughly triangular in outline.

No upper incisors are present in the jaws, but two such incisors are apparently associated. They appear to be similar to the lower incisors, but have not been figured because of the lack of positive association. The course of the alveolus is shown in M.A.C.N. no. A 52-89. It is curved to about the same extent as in *Neoreomys,* but does not extend as far posteriorly, ending a short distance behind the maxillo-premaxillary suture and thus well in front of the anterior root of the zygoma. Its posterior extremity descends farther ventrally, however, than in the Santa Cruz form.

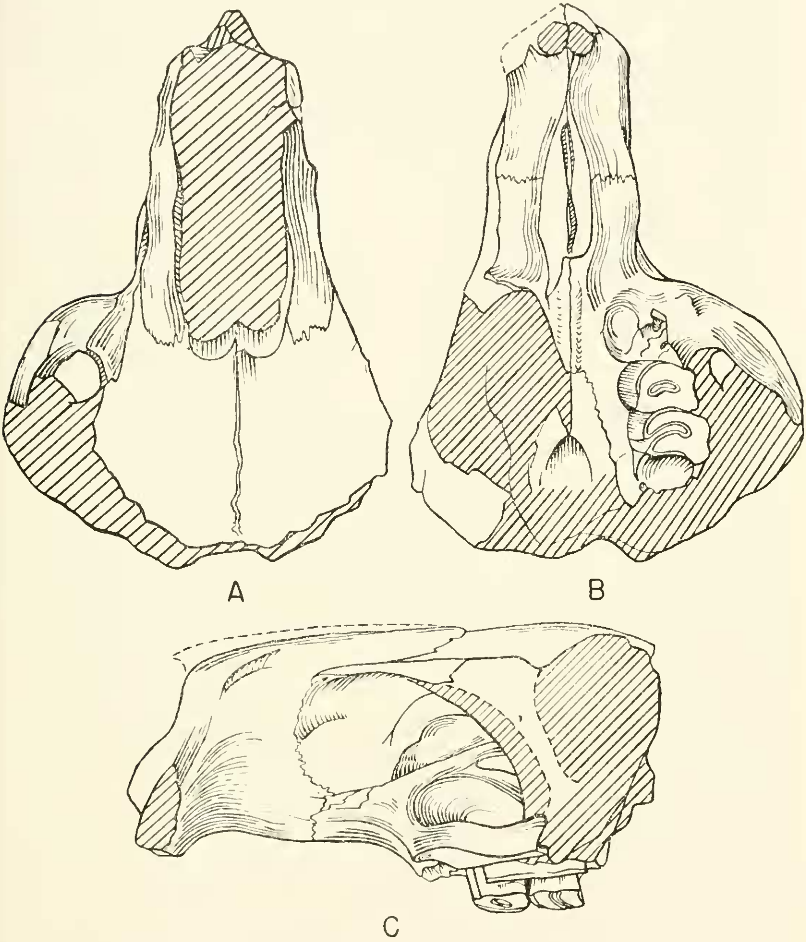

Fig. 21. *Cephalomys arcidens* Ameghino. Facial region of skull, M.A.C.N. no. A 52-89; *A* dorsal, *B* ventral, *C* right lateral view, x 2. Crosshatching indicates matrix; position of infraorbital foramen shown in dashed outline in *C*.

Skull and Mandible

Various specimens, M.A.C.N. no. A 52-89, A.C.M. nos. 3066, 3085, 3091, 3099, 3274 and A.M.N.H. no. 29558, combine to furnish some information concerning the skull. By far the most complete of these is M.A.C.N. no. A 52-89, consisting of the greater part of the facial region. This is the ''skull'' mentioned by Ameghino in his original description (1897c, p. 494) and the following account is largely based on it.

The rostrum (Fig. 21) is relatively narrow and nearly parallel-sided; it is shorter, but otherwise rather similar to that of *Platypittamys,* and decidedly narrower than the rostrum of *Neoreomys.* The nasals are missing. They extended as far posteriorly as in *Neoreomys,* and the suture between them and the frontals is nearly as transverse; the only notable difference between the two forms in this area is that the frontal in *Cephalomys* sends forward a small wedge between the premaxillary and the nasal. The position of the suture relative to the dorsal root of the zygoma was clearly very similar in both. The frontals are extremely flat, even those parts above the orbits not curving downward to any marked extent. The maxillo-frontal suture, transverse in *Neoreomys,* is here almost longitudinal in direction, due to a narrow triangular projection from the frontal that runs forward between the premaxillary and maxillary. Posterior to this projection, the edge of the frontal shows a somewhat ribbed ventral surface, which suggests the sutural area for the lachrymal. If this indication is correctly interpreted, the size and relations of the latter bone must have been much as in *Neoreomys.* Behind this supposed sutural surface, the upper margin of the orbit is more sharply excavated than in *Neoreomys.* In all probability a postorbital process was present, as in Caviomorpha generally, but the specimen ends at a point just anterior to where this structure would begin.

The premaxillary is similar in general to that of *Neoreomys.* Anteriorly, it sends forward a thin median projection in advance of the incisor alveoli, a feature barely indicated in the Santa Cruz form. The dorsal process is stout, and extends back almost as far as the level of the fronto-nasal suture. The lateral surface of the bone, in decided contrast to *Neoreomys,* is not involved in the masseteric fossa on the side of the rostrum. The ventral surface is about as wide, proportionately, as in *Neoreomys*, the expansion of the rostrum in the latter having taken place in the dorsal portion, evidently *pari passu* with the forward extension of the masseteric fossa. The incisive foramina are wide, much wider than in *Neoreomys*, and lie together in a fossa that deepens posteriorly in its maxillary portion, the posterior wall sloping sharply posteroventral to the palate. The fossa extends back almost to the level of P^4 and slightly beyond that of the anterior root of the zygoma (Fig. 22B). Precisely similar conditions do not appear to exist in any Santa Cruz rodents.

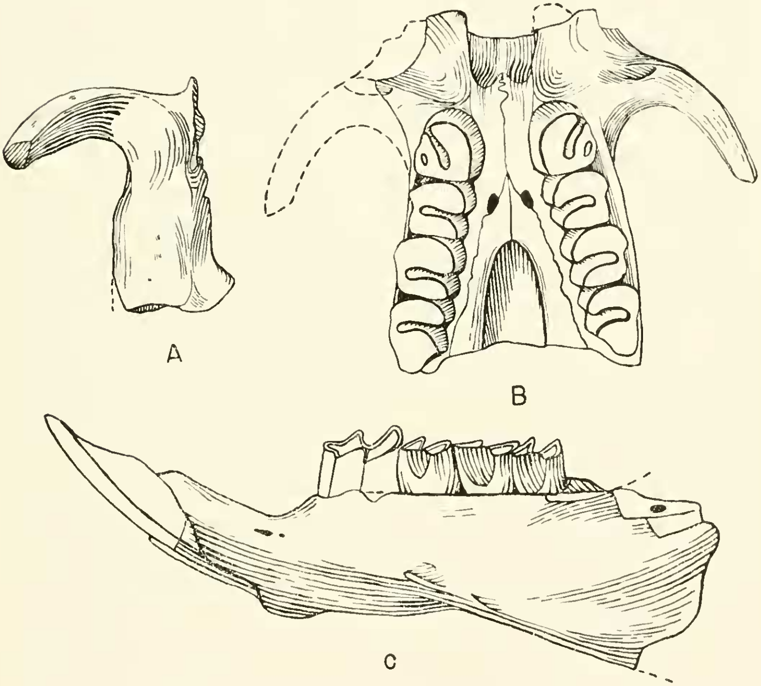

Fig. 22. *Cephalomys*. *A*, *Cephalomys plexus* Ameghino, dorsal view of left maxilla, A.C.M. no. 3085; *B*, *Cephalomys* sp., ventral view of palate, A.C.M. no. 3109 (detail between tooth rows restored from A.C.M. no. 3091, *C. plexus*), x 3. *C*, *Cephalomys arcidens*, lateral view of mandible, A.C.M. no. 3058 (parts in outline from A.C.M. no. 3005, *C. plexus*), x 2.

The palate is very compressed, being narrowest between the premolars and gradually widening (Fig. 22B), as in *Myocastor* and *Olenopsis?* (Fields, 1957, Fig. 15). The posterior widening is much more marked than in *Neoreomys* but less so than in *Perimys.* A deep notch, extending as far forward as the middle (*C. arcidens*) or even the front (*C. plexus*) of M^2, marks the posterior border of the palate. Such a deep notch is not present in *Neoreomys* nor in any other Santa Cruz rodent figured by Scott except *Stichomys* (Scott, 1905, Pl. 65, fig. 17); there is no posterior median projection of the palate. The palatine extends parallel to the margin of this notch, its anterior limit being near the front of M^1 (Figs. 21B, 22B). The posterior palatine foramina lie very close to the midline beside the anterior tip of the palatines, which they may indent very slightly (Fig. 22B). In this, they differ from *Neoreomys*, in which the foramina notch the palatines so deeply "as to be almost entirely enclosed in them" (Scott, 1905, p. 394).

The greater part of the zygomasseteric region is preserved, and what is missing may be inferred with confidence from what is present (Figs. 21-22). The anterior root of the zygoma is somewhat variable in size in some specimens of *C. arcidens,* extending from well in front of P^4 to a point external to M^1, but in some of *C. plexus* not extending behind P^4. The ventral surface of the arch is gently concave, with a sharply crested external margin and a rounded internal one that becomes less pronounced posteriorly. Anterointernally there is a small but clearly defined ventral projection, on the posterior slope of which is a very slightly roughened area, prominent in some specimens of *C. plexus,* that is set off a little from the surrounding bone. It seems very likely that this marks the place of origin of the tendon of M. masseter superficialis. M. masseter lateralis clearly originated from the concave under surface of the arch, and M. masseter medialis, pars posticus, probably had its origin along the medial border. The relations of these portions of the muscle mass would appear to have been essentially similar to those of *Chinchilla* (Wood and White, 1950, pp. 552-554, Figs. 2-3). The dorsal side of the ventral root is very robust, arching strongly upward from front to back. Its posterior surface passes medially into a raised area on the side of the maxillary above P^4-M^1. The arch is preserved to a point opposite M^2 in M.A.C.N. no. A 52-89, and at its posterior extremity the dorsal margin begins to turn upward, thus marking the beginning of the ventral part of the lateral wall of the infraorbital foramen (Fig. 21C). In *Neoreomys* the upturn begins opposite M^1. The fenestra, therefore, was relatively larger in the Oligocene form than in the Miocene one, a fact of some interest, as will appear. The infraorbital nerve and blood vessels evidently ran forward medial to the raised area on the side of the maxillary, where there is a groove (Fig. 22A), and reached the rostrum via the ventral part of the infraorbital foramen. The lateral surface of the rostral portion of the maxilla is occupied by the masseteric fossa mentioned above, which extends anteriorly as far as the maxillo-premaxillary suture (Fig. 21C). Within the fossa, the naso-lachrymal canal is large and prominent, similar in general to that of *Neoreomys* and *Dasyprocta*. Dorsally, the fossa is roofed, as in most caviomorphs, by a thin lateral extension from the upper part of the maxillary, which progressively increases in width posteriorly. This extension is broken off at the level of the naso-frontal suture, but obviously it continued downward and backward to join the upturned part of the zygomatic portion of the maxillary and thus formed, together with the lachrymal, the lateral wall of the infraorbital foramen (Fig. 21C). The fossa clearly served for the reception of M. masseter medialis, pars anticus.

Wood (1949, pp. 13, 49-50) has suggested that enlargement of the infraorbital foramen did not accompany but preceded the forward migration of the anterior portion of the deep masseter to the rostrum. Conditions in *Platypittamys,* in which there is a foramen of moderate size, much smaller than in other caviomorphs, and no indication of a fossa in the side of the rostrum, certainly appear to indicate that this was the case. *Cephalomys* is clearly a more advanced form. As noted above, the infraorbital foramen of *Cephalomys* is relatively larger than that of the later *Neoreomys.* Despite this, the fossa in the rostrum is smaller, extending anteriorly to the maxillo-premaxillary suture, whereas that of the Santa Cruz form extends far on to the premaxillary (Scott, 1905, Pl. 64, fig. 6a). It seems evident that the part of the masseter that had its origin in the fossa in *Cephalomys* must have been smaller than the corresponding part in *Neoreomys.* As in *Platypittamys,* it is therefore probable that enlargement of the foramen preceded, or at least more than merely kept pace with, the forward migration of the muscle. This is not the only interesting inference to be drawn from the available facts. *Platypittamys,* in which the masseter had not begun, or at most had just begun, to pass off the ventral surface of the zygoma, is an octodontid; *Cephalomys,* in which the migration is in full progress, is a dasyproctid. It would therefore appear that in the ancestral caviomorph stock: 1) there was an infraorbital foramen of moderate proportions; 2) M. masseter medialis, pars anticus, was of protrogomorph type; 3) this combination provided the structural basis for the acquisition of the caviomorph zygomasseteric structure; and 4) the advanced stages of this structure were acquired independently in the various groups that rapidly diverged from the ancestral stock. It is now, we believe, virtually certain that the resemblances between caviomorphs and hystricomorphs in zygomasseteric structure are the result of parallel evolution.

Several mandibles, one or two quite complete, are known. The ventral part of the mandible is broadened, as in *Cavia, Cuniculus, Neoreomys, Dasyprocta* and *Lagostomus,* but is quite different from the conditions in *Chinchilla, Coendou* or *Erethizon.* This thickening is lateral to the roots of the cheek teeth, and is apparently related to the development of a more efficient insertion for the masseter. The lower incisor lies on the lingual side of the roots of the cheek teeth, its posterior end being below or nearly below M_3. The diastema is rather short. The mental foramen is high on the ramus, nearly at the alveolar border of the diastema, and well forward of the cheek teeth. There is some uncertainty as to the coronoid process. M.A.C.N. no. A52-104, *C. plexus,* the specimen figured by Ameghino, shows a thin ridge of bone running from a point external to the posterior half of M_3 to the base of the condyle and scarcely rising to the level of the molars. There is no trace of an elevation on the ridge, although a small process could have been broken off. Loomis (1914, p. 191, Fig. 121) figures and describes a small coronoid. His figure was apparently based on A.C.M. no. 3005, *C. plexus,* but this specimen is now broken off behind M_3. A.C.M. no. 3058, *C. arcidens* (Fig. 22C), suggests that a coronoid may have been present. The mandibular foramen is large.[16] The condyle is oval,

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[16] Ameghino shows a minute foramen beneath the mandibular foramen, within the pterygoid fossa. Examination of the figured specimen (M.A.C.N. no. A 52-104) does not support this. The jaw is cracked in this region, and the supposed foramen appears to be a local enlargement within the crack. Other specimens show no foramen in this position.

laterally compressed, faces dorsally, and is but little above the level of the cheek teeth. Below it, and continuing from its posterior margin, is a delicate right-angled process. The structure of this part of the mandible is rather different from that of *Neoreomys*,[17] in which the condyle is higher. Although the angle is broken off in all available material, the beginning of it is present in A.C.M. no. 3059, showing it to have been inflected. The symphysis is very extensive, running the entire length of the receding chin, as in *Erethizon*, but is rather corrugated, indicating a relatively firm union of the two mandibles. This varies between the species. The geniohyal pit is very weak. Near the anterior end of the masseteric fossa is a pit for the attachment of the masseter. The chin region bears a considerable number of nutritive foramina, as in *Eutypomys* (Wood, 1937a, Pl. 29).

SPECIES

The species of *Cephalomys* are not as readily distinguishable as would appear at first glance. Due to their hypsodonty, the details of the tooth pattern are rapidly lost with wear, and only the generic pattern remains. A few possible characters have been mentioned above. Ameghino's distinctions were based largely on size. Initially we thought that three species were represented. However, on plotting the greatest length against the greatest width for each tooth, two size groups appeared. These are quite separate except for one individual, initially referred to *C. plexus* (A.C.M. no. 3109, a palate with all eight cheek teeth; Figs. 14C, 22B, Table 6), which falls in the smaller group for P^4, occupies an intermediate position as regards M^{1-2}, although somewhat nearer the smaller group, and falls in the larger group for M^3. A few other specimens that appear to be intermediate in size are clearly very old individuals of the larger species, *C. arcidens*, the small size being due to the fact that the widest parts of the crown have been worn away. The statistical analysis for the larger species, *C. arcidens* (Tables 3-4) shows that it is a homogeneous population (V usually in the range 6-10). This is true even

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[17] While on the subject of the jaw of *Neoreomys*, we may mention that this genus does not possess the "wide, shelflike masseteric ridge extending back along the angular process" (Landry, 1957a, p. 45) which might be expected of it if it were closely related to *Myocastor*. *Neoreomys* is actually very much like *Dasyprocta* in this respect, the ridge in both being of modest proportions.

though the measurements of maximum tooth diameter, maximum extra-alveolar diameter, and diameter of wear surface were lumped (Tables 3-4). An analysis of two of the three types of measurements taken separately and all three lumped (Table 3) showed that their means and standard deviations coincided within the overlap of their standard errors. Similar investigation of the less numerous, smaller species, *C. plexus* (Table 5) showed about the same situation for the lower teeth, but gave extreme variation in the upper teeth (with the SD reaching 20 per cent of the mean, and V reaching 22.07) when A.C.M. no. 3109 was included. When this specimen was excluded, the statistics of the upper teeth of *C. plexus* correspond with those of the other sets of teeth. It is therefore concluded that there are two valid species, *C. arcidens* and *C. plexus*, and that A.C.M. no. 3109 is an anomalous individual that requires separate treatment. Its measurements are given in Table 6.

Regression lines were computed for the length, x, versus metalophid width, y, of M_2. These gave regression coefficients for the two species which showed no significant difference, the only distinction in the regression lines being the size of the species. The regression coefficients are: *C. arcidens*, $b_{yx} = .658$, $b_{xy} = .667$; *C. plexus*, $b_{yx} = .765$, $b_{xy} = .703$.

It might be worth mentioning that the coefficient of variation (V) of *Cephalomys* is much greater than that computed for brachyodont rodent teeth (particularly a series on members of the Paramyidae), which is certainly related to the much greater hypsodonty of *Cephalomys* and the corresponding inability to measure with certainty the maximum diameters, except on isolated teeth.

As indicated, the variation in tooth measurements is partly due to wear. The widest point of the tooth is near the middle, vertically. Therefore, old individuals show smaller measurements of maximum transverse width than do younger ones. Very young individuals also show smaller measurements if the teeth are in jaws, since the widest point may be within the alveoli. In the anteroposterior measurement, there is extensive interdental wear after the enamel is interrupted, and the teeth become markedly shortened with further use. Processes of this sort, together with long-continued growth, rather than tooth growth anywhere except at the base of the crown, are, we feel certain, the basis for the anomalous results reported by Fields (1957, pp. 354-355) for late Miocene dinomyids.

The possibility has been considered, and can by no means be ruled out, that these two groups represent the two sexes. In general, however, sexual size differences among rodents do not appear to be as great as the differences between these two groups. Moreover, it would seem reasonable to expect more nearly equal representation of the two sexes in a sample of this magnitude than is the case with the two size groups.

It seems probable to us that these differences are of taxonomic significance and that two forms are present. The presence of the unusual individual, A.C.M. no. 3109, rather complicates the picture, in that it shares size features with both groups. This could be explained as merely an extreme in the variation of either group except for the statistical studies. It might also be a hybrid, if specific crosses were possible in *Cephalomys*. The possibility also exists that A.C.M. no. 3109 is an isolated representative of a third species, occupying a different habitat from that in which the other two species lived and were buried.

CEPHALOMYS ARCIDENS Ameghino 1897

Figs. 13, 14A-B, 15B-C, 16, 18, 19A-D, 20 and 21

Cephalomys arcidens Ameghino 1897c, p. 494; 1906, p. 414, Fig. 292; Loomis 1914, pp. 189-190, Figs. 118-119; Schaub, *in* Stehlin and Schaub 1951, Fig. 396, p. 246.

Cephalomys prorsus Ameghino 1903a, p. 95, Fig. 11, p. 98, Figs. 14, 16, p. 99 (in part, not including the type).

Orchiomys prostans Ameghino 1897c, p. 495.

Syntypes. M.A.C.N. no. A 52-88, right and left palatal fragments with P^4-M^3, left mandible with P_4-M_3 and root of I; M.A.C.N. no. A 52-89, facial region of skull with alveoli of R and L I, alveoli of LP^4, M^3 and LM^{1-2}. M.A.C.N. no. A 52-88, Ameghino's figured specimen, is here designated as lectotype.

Type of Orchiomys prostans. M.A.C.N. no. A 52-96, fragment of right mandible with posterior part of dm_4, M_{1-2}.[18]

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[18] Ameghino (1897c, p. 495) referred to the two complete teeth as the fourth and fifth molars, i.e. as P_4-M_1, which is certainly not the case. Earlier (1896, 1897b), he had declared that the Deseadan rodents had five lower cheek teeth, a statement that he soon corrected (1897c, p. 494, footnote), declaring that he had based it on a specimen in which the anterior part of the milk molar was preserved together with the corresponding premolar. The type of *O. prostans* may have been the specimen in question, with "anterior end of the milk molar" being a lapsus for posterior end, and M_1 mistaken for P_4; certainly there is no other specimen now in the Ameghino Collection on which the error could possibly have been based.

Hypodigm. The types listed above, and an additional series of good specimens: six in the Ameghino Collection, twenty-eight in Amherst, twelve in the Muséum National d'Histoire Naturelle, three in Chicago Natural History Museum, six in The American Museum of Natural History, five in the Yale Peabody Museum and two in the Museum of Comparative Zoology. The more important of these are mentioned in the account of the morphology or identified in the figure captions. In addition there are numerous isolated first and second molars and incisors that have not been used in the statistical investigation.

Horizon and localities. Deseadan. The Muséum National specimens are from La Flecha, Santa Cruz; those in the Amherst, Chicago, Yale, Museum of Comparative Zoology and American Museum collections are from Cabeza Blanca, Chubut. Ameghino gave no localities for his specimens, but to judge from their appearance, it is probable that all of them are from Cabeza Blanca. One lot of isolated teeth in the Ameghino Collection, M.A.C.N. no. A 52-97, has an accompanying label reading ''Gran yacimiento del Pyroterio — Río Chico,'' which surely indicates this locality.

TABLE 3

Comparison of measurements (in mm.) for occlusal diameter and maximum diameter of lower cheek teeth of *C. arcidens*

	N	M	SD	V
P_4 anteroposterior				
diameter of occlusal surface	24	4.33±.06	.31±.04	7.16±1.03
maximum diameter of crown	12	4.45±.09	.30±.06	6.74±1.38
Total, all specimens	37	4.38±.05	.32±.04	7.31± .85
width hypolophid				
diameter of occlusal surface	14	3.24±.09	.32±.06	9.88±1.87
maximum diameter of crown	16	3.46±.12	.47±.08	13.58±2.40
Total, all specimens	34	3.38±.07	.42±.05	12.43±1.51
M_1 width hypolophid				
diameter of occlusal surface	10	3.07±.04	.12±.03	3.91± .87
maximum diameter of crown	17	3.12±.08	.32±.05	10.26±1.76
Total, all specimens	29	3.10±.05	.26±.03	8.39±1.10
M_3 width metalophid				
diameter of occlusal surface	10	3.00±.06	.19±.04	6.33±1.42
maximum diameter of crown	10	3.16±.08	.26±.06	8.23±1.84
Total, all specimens	24	3.11±.05	.24±.03	7.72±1.11

Statistics not run on specimens where measurement was ''greatest extra-alveolar diameter,'' since in all cases there were fewer than 10 specimens.

TABLE 4

Tooth measurements (in mm.) of *Cephalomys arcidens*

		N	Observed Range	M	SD	V	Lectotype, M.A.C.N. no. A 52-88
P^4-M^3		7	12.6-14.2	13.6			
P^4	anteroposterior	20	3.16-4.29	3.63±.06	.26±.04	7.16±1.13	3.61
	width, protoloph	15	2.87-3.71	3.38±.06	.25±.05	7.40±1.35	
	width, metaloph	15	3.09-4.80	3.55±.06	.25±.05	7.04±1.29	4.80†
M^1	anteroposterior	16	2.53-3.32	3.08±.05	.20±.04	6.49±1.15	3.32
	width, protoloph	14	2.97-4.29	3.25±.04	.16±.03	4.92±.93	4.07†
	width, metaloph	14	2.71-3.37	3.03±.05	.18±.03	5.94±1.12	
M^2	anteroposterior	12	2.83-3.36	3.06±.05	.18±.04	5.88±1.20	3.28
	width, protoloph	10	3.25-4.62	3.45±.04	.12±.03	3.48±.78	4.39†
	width, metaloph	10	2.96-3.58	3.20±.07	.21±.05	6.56±1.47	
M^3	anteroposterior	9	2.58-3.23	2.94			3.19
	width, protoloph	8	2.86-4.29	3.18			4.12†
	width, metaloph	8	2.22-3.27	2.74			
I^1	anteroposterior	3	2.45-2.90	2.61			
	transverse	3	1.79-2.20	1.95			
P_4-M_3		5	14.9-17.5	15.6			
P_4	anteroposterior	37	3.67-4.92	4.38±.05	.32±.04	7.31±.85	4.50
	width, metalophid	20	2.53-3.57	3.19±.06	.27±.04	8.46±1.34	
	width, hypolophid	34	2.04-4.23	3.38±.07	.42±.05	12.43±1.51	2.90†
M_1	anteroposterior	26	2.62-3.88	3.22±.05	.25±.03	7.76±1.08	2.90
	width, metalophid	21	2.74-3.52	3.12±.05	.25±.04	8.01±1.24	3.01†
	width, hypolophid	29	2.43-3.63	3.10±.05	.26±.03	8.39±1.10	
M_2	anteroposterior	22	2.96-3.66	3.30±.04	.21±.03	6.36±.96	3.10
	width, metalophid	22	3.00-3.73	3.35±.04	.21±.03	6.27±.95	3.24†
	width, hypolophid	14	2.99-3.77	3.35±.06	.23±.04	6.87±1.30	
M_3	anteroposterior	22	2.67-3.63	3.02±.06	.26±.04	8.61±1.30	2.67
	width, metalophid	24	2.70-3.67	3.11±.05	.24±.03	7.72±1.11	2.70†
	width, hypolophid	14	2.40-3.27	2.74±.07	.25±.05	9.12±1.72	
I_1	anteroposterior	13	1.96-2.60	2.19±.06	.21±.04	9.59±1.88	
	transverse	15	1.72-2.35	1.99±.05	.20±.04	10.05±1.83	
dm_4	anteroposterior	2	4.70-4.78	4.74			
	width, hypolophid	3	2.25-2.30	2.28			

Means computed on all measurements ; other statistics only when $N>9$.

Diagnosis. Largest known species of the genus (Tables 3-4); anteroconid of P_4 a rounded enlargement in middle of anterolophid when unworn. In addition, several possible differences based on one or two individuals have been mentioned above in the description of the genus.

Ameghino's reference of two specimens of this species to *Cephalomys prorsus* (a synonym of *C. plexus*) was probably a lapsus. The specimens in question — M.A.C.N. no. A 52-94, a mandible, and M.A.C.N. no. A 52-95, an isolated P_4 and dm_4 — fall within the size range of *C. arcidens,* and this is evident not only from our very large series but also from the much smaller one that was available to Ameghino. M.A.C.N. no. A 52-94 is, in fact, approximately the same size as the lectotype of *C. arcidens.* "*Orchiomys prostans*" was based on a young individual of *C. arcidens,* in which M_1 is at stage 3 and M_2 at stage 2. The lectotype of *C. arcidens* happened to be an old individual with M_1 at stage 6 and M_2 at stage 5. Ameghino did not visualize the differences resulting from wear; his identification of M_{1-2} of "*O. prostans*" as P_4-M_1 may indeed have prevented him from doing so.

This is the most abundant Deseadan mammal (Loomis, 1914, p. 189), being represented by over 100 individuals, counting isolated teeth, in the collections we have studied. In the unworn P_4, the anteroconid is connected primarily with the middle or the lingual part of the metalophid. This may be its only connection (A.C.M. no. 3161, Fig. 19A and no. 3162), or there may be another one with the protoconid (A.C.M. no. 3108, Fig. 18A). The enamel, as already pointed out, is interrupted on the anterior face of the lower molars (Fig. 19D) and the buccal and posterior faces of the upper molars after considerable wear. There do not appear to be any other interruptions.

CEPHALOMYS PLEXUS Ameghino 1897
Figs. 14D, 15A, 16E-F and 22A

Cephalomys plexus Ameghino 1897c, p. 494; 1906, p. 421, Fig. 314; Loomis, 1914, pp. 190-191, Figs. 120-122; Stehlin and Schaub, 1951, Fig. 76, p. 61; Schaub, *in* Stehlin and Schaub, 1951, p. 245, Fig. 394.

Cephalomys prorsus Ameghino, 1899, p. 560, Fig. 6; 1902b, p. 37; 1902d, p. 425, Fig. 6; 1903a, p. 82, Fig. 1, p. 96, Fig. 12, pp. 122-123, Figs. 41-42; Schaub, *in* Stehlin and Schaub, 1951, Fig. 395, p. 245.

Cephalomys prosus [*sic*] Loomis 1914, pp. 191-192, Figs. 123-124 (lapsus for *C. prorsus* Ameghino).

Asteromys prospicuus Ameghino 1897c, p. 495.
Asteromys annectens Ameghino 1902b, p. 37.

Syntypes. M.A.C.N. no. A 52-99, portion of right maxillary with P^4-M^3; M.A.C.N. no. A 52-100, portion of left maxillary with P^4-M^3; M.A.C.N. no. A 52-101, portion of right mandible with P_4-M_2; M.A.C.N. no. A 52-102, portion of left mandible with P_4-M_2. M.A.C.N. no. A 52-99, the only one of the series subsequently figured by Ameghino, is here designated as the lectotype.

Types of synonyms. Cephalomys prorsus. M.A.C.N. no. A 52-103, portion of right mandible with P_4 not yet fully erupted and $M_{1\text{-}3}$.[19] *Asteromys prospicuus.* M.A.C.N. no. A 52-107, four isolated upper molars, one LM^3, one $LM^{1 \text{ or } 2}$, one $RM^{1 \text{ or } 2}$ and one fragment. LM^3, the only tooth that actually comes within the size range given by Ameghino, is hereby designated as the lectotype. *Asteromys annectens.* M.A.C.N. no. A 52-108, portion of the left mandible with I, P_4-M_3, and M.A.C.N. no. A 52-109, palate with R and L P^4-M^3; M.A.C.N. no. A 52-108 is here designated as the lectotype.

Hypodigm. The types listed above and a series of good additional specimens, three in the Ameghino collection, seventeen in Amherst, one in the Muséum National d'Histoire Naturelle, one in Chicago Natural History Museum, two in The American Museum of Natural History and four in the Yale Peabody Museum. As in the case of *C. arcidens*, there are, in addition, numerous isolated teeth.

Horizon and localities. Deseadan. The Muséum National specimens are from La Flecha, Santa Cruz; those in the Amherst, Chicago, Yale and American Museum collections are from Cabeza Blanca, Chubut. Again, as in the case of *C. arcidens*, it is probable that Ameghino's specimens were obtained at Cabeza Blanca.

Diagnosis. Approximately two-thirds the size of *C. arcidens* (Table 5); apex of anteroconid of P_4 distinct from anterolophid when unworn.

Cephalomys "prorsus" was distinguished from *C. plexus* on the basis of slightly smaller size and on the following structural

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[19] *C. prorsus* was formally proposed as new by Ameghino in 1902b, p. 37, and the diagnosis there given was based on this specimen and on M.A.C.N. nos. A 52-104 and A 52-105. Previously, however, he had described and figured M_3 of M.A.C.N. no. A 52-103 under this name (1899, p. 560, Fig. 6). The earlier account is sufficient to date the name from 1899 and to fix the type as M.A.C.N. no. A 52-103.

TABLE 5

Tooth measurements (in mm.) of *Cephalomys plexus*

		N	Observed Range	M	SD	V	Lectotype M.A.C.N. no. A 52-94
P^4-M^3		4	7.50-9.60	8.91			
P^4	anteroposterior	10	2.10-2.90	2.45±.08	.26±.06	10.61±2.37	2.40
	width, protoloph	5	1.90-2.96	2.30			
	width, metaloph	9	2.12-3.04	2.68			2.89†
M^1	anteroposterior	13	1.82-2.45	2.24±.05	.18±.04	8.04±1.58	2.02
	width, protoloph	12	1.97-2.74	2.40±.08	.26±.05	10.83±2.21	2.70†
	width, metaloph	7	1.72-2.57	2.07			
M^2	anteroposterior	11	2.03-2.72	2.23±.06	.20±.04	8.97±1.91	2.10
	width, protoloph	11	2.07-2.98	2.48±.08	.25±.05	10.08±2.15	2.51†
	width, metaloph	6	1.88-2.40	2.21			
M^3	anteroposterior	11	1.72-2.28	1.96±.05	.15±.03	7.65±1.63	1.91
	width, protoloph	11	1.82-2.46	2.16±.07	.22±.05	10.19±2.17	2.28†
	width, metaloph	5	1.36-1.88	1.63			
P_4-M_3		4	9.65-11.68	10.57			
P_4	anteroposterior	9	2.45-3.53	2.90			
	width, metalophid	4	1.74-2.63	2.20			
	width, hypolophid	9	1.81-3.10	2.28			
M_1	anteroposterior	12	2.04-2.76	2.41±.06	.22±.04	9.13±1.86	
	width, metalophid	7	1.96-2.85	2.30			
	width, hypolophid	12	1.89-2.82	2.29±.08	.26±.05	11.35±2.32	
M_2	anteroposterior	10	2.20-2.63	2.38±.05	.15±.03	6.30±1.41	
	width, metalophid	10	2.05-2.51	2.31±.05	.16±.04	6.93±1.55	
	width, hypolophid	5	2.30-2.36	2.33			
M_3	anteroposterior	11	1.68-2.50	2.14±.07	.22±.05	10.28±2.19	
	width, metalophid	11	1.71-2.31	2.11±.05	.17±.04	8.06±1.72	
	width, hypolophid	7	1.32-1.96	1.77			
I_1	anteroposterior	6	1.44-1.57	1.52			
	transverse	6	1.16-1.39	1.28			

† = Greatest extra-alveolar diameter.
Means computed on all measurements; other statistics only when N>9.

TABLE 6

Tooth measurements (in mm.) of *Cephalomys* sp., A.C.M. no. 3109

		Left	*Right*
P^4-M^3		11.0	
P^4	anteroposterior	2.42	2.40
	width, protoloph	2.53	2.27
	width, metaloph	2.86	2.51
M^1	anteroposterior	2.33	2.42
	width, protoloph	2.99	2.89
	width, metaloph	2.33	2.47
M^2	anteroposterior	2.39	2.55
	width, protoloph	2.82	2.78
	width, metaloph	2.37	2.44
M^3	anteroposterior	3.10	3.19
	width, protoloph	2.89	2.76
	width, metaloph	2.09	2.33

characters: 1) anterior lobe of lower molars more compressed anteroposteriorly and more pointed at the extremities, 2) posterior lobe of lower molars with a more convex posterior face, and 3) upper molars with small, isolated enamel fossettes. The difference in size is not significant. The first two features are due in part to age and in part to individual variation; specimens structurally intermediate exist, even in the Ameghino Collection. Item 3) has no significance whatever, being entirely an age character; these fossettes may also be seen in Ameghino's syntype series of *C. plexus*.

"*Asteromys prospicuus*" was not, of course, contrasted with *C. plexus* by Ameghino, and the only character he gave to separate it from *Asteromys punctus* was the small size of the upper molars, 1.6 to 1.8 mm. in length. Since *A. punctus* was based on a mandible, no real basis for comparison existed. The syntypes of "*A. prospicuus*" are upper molars of *Cephalomys* at stage 5. Their sizes (length of LM^3 1.8, of LM^{1-2} 2.0, and of $RM^{1 \text{ or } 2}$ 2.4 mm.) are within the range of *C. plexus* and there can be no doubt as to the synonymy.[20]

[20] In the same labeled box with the molars of *A. prospicuus* was another upper tooth, M.A.C.N. no. A 52-87 (described here on p. 376), that is very different from the syntypes and does show some resemblance in crown structure to the lower molars of *A. punctus*, although much lower-crowned. This tooth may have decided Ameghino that he was dealing with an *Asteromys*, but it cannot be selected as the lectotype and the other molars excluded from the species. It is over 3 mm. in length, and this is too great a difference from the measurements given by Ameghino to be attributed to the cruder measuring devices and optical aids available in 1897.

"*Asteromys annectens*" was described as being transitional between *Asteromys* and *Cephalomys*. In reality, the syntypes are indistinguishable from *C. plexus* either in size or in structure. In the lectotype mandible, M_{1-2} are at stage 4, and M_3 at stage 2. P^4 is at stage 2, M^{1-2} at stage 5, and M^3 at stage 4.

The differences, other than size, separating *C. plexus* from *C. arcidens* are difficult to detect. The distinction in the anteroconid of P_4 can be seen only in unworn teeth. With wear, there are interruptions of the enamel at the posterointernal corners of the lower molars, which occur before the interruptions on the anterior face (Fig. 19F). In the upper cheek teeth there is some variation. In most specimens, the enamel is interrupted first along the buccal side and subsequently along the posterior face, as in the anomalous specimen, A.C.M. no. 3109 (Fig. 14C). In one specimen, A.C.M. no. 3085 (Fig. 14D), which is at the lower limit of the size range, the interruption appears to take place at a much later stage in the wear, as indicated by the difference in pattern of P^4. In this specimen, however, the enamel along the buccal and posterior margins of the teeth is considerably thinner than elsewhere.

LITODONTOMYS Loomis 1914

Litodontomys Loomis 1914, p. 193.

Type species. L. chubutensis Loomis 1914.

Distribution. Deseadan, Patagonia.

Emended diagnosis. Cheek teeth high-crowned, cement present in flexids, enamel not extending to bases of teeth on anterior and lingual faces; P_4 not molariform, elongate; para- and metaflexids shallow (obliterated by wear on only known specimen), mesoflexid not as deep as hypoflexid, converting to fossettid with deep wear.

LITODONTOMYS CHUBUTENSIS Loomis 1914

Fig. 23

L. chubutensis Loomis 1914, p. 194, Fig. 127.

Type. A.C.M. no. 3086, fragmentary right mandible with I, P_4-M_3.

Hypodigm. Type only.

Horizon and locality. Deseadan, Cabeza Blanca, Chubut.

Diagnosis. As for the genus; for measurements see Table 7.

The teeth are evidently not typically brachyodont, as Loomis believed, but are fairly well along the road toward high crowns. They appear low, however, due to the excessive wear that they have undergone. This interpretation is based on the fact that cement is present, that the enamel is interrupted on the anterior and lingual sides of the teeth, and that there is a considerable difference in the crown height of M_1 and P_4, on the one hand, and M_3, on the other. In many respects, this form appears to us to be one of the more specialized of the Deseadan rodents. The hypoflexids are directed just posterad of the mesoflexids.

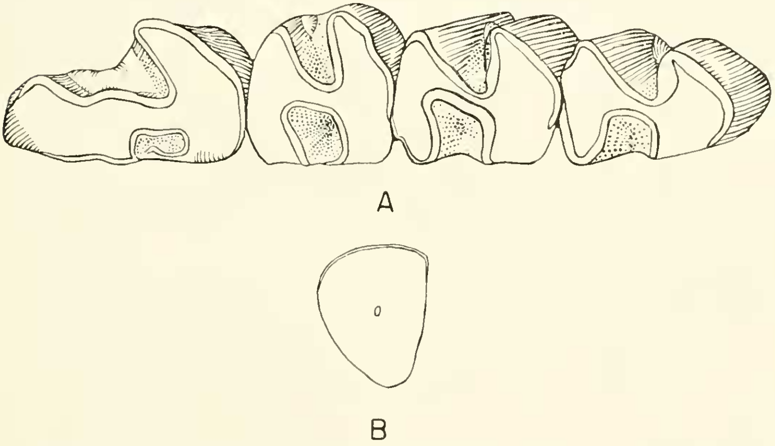

Fig. 23. *Litodontomys chubutensis* Loomis, type, A.C.M. no. 3086, x 10. *A*, RP_4-M_3; *B*, cross-section of RI_1, anterior view.

The premolar has what appears to be a simple talonid (although a shallow metaflexid or -fossettid may have been present originally) connected with an anteroposteriorly expanded trigonid by an ectolophid that widens near its anterior end (Fig. 23A). The mesoflexid is considerably smaller than the hypoflexid, both trigonid and talonid sending arms along the lingual margin of the tooth, which meet, closing off a cement-filled mesofossettid at the present stage of wear. The hypoflexid is much larger, and extends low down on the side of the tooth, as a broad, open embayment. It is partially blocked by a low cingulum, and is partially filled with cement. Enamel is absent over the anterior face of the tooth and from the lingual surface of the talonid, in both cases obviously due to original non-deposition near the base of a high-crowned tooth (Wood, 1940, pp. 356-357), and not due to interdental wear (H. E. Wood, 1938). The free end of the enamel plate on the lingual margin of the tooth apparently is embedded in the dentine.

The molars are made up of two nearly equal lobes, although the talonid is somewhat the larger in each case. The flexids are of more nearly the same size than in P_4, though the hypoflexids are somewhat larger than the mesoflexids in each case. In M_1, both flexids are nearly filled with cement. The mesoflexid is closed, as in P_4, by arms from the internal cusps, whereas the hypoflexid appears to slope to the base of the tooth, being filled with cement. Enamel is absent along the anterior and lingual faces of the tooth and the lingual part of the posterior face.

The mesoflexid of M_2 appears to be of about the same depth as that of M_1 of this specimen. Since the tooth is less worn than M_1, this means that the mesoflexid was actually shallower. The hypoflexid is quite deep. The lingual fold extends as a groove down the side of the tooth, the cingulum closure not being quite at the lingual margin of the valley. Enamel is missing from that part opposite the enamel-bearing portion of M_1 and is present on that part opposite the enamel-free section. It is also missing on part of the lingual border of the talonid, as in geomyoids (Wood, 1937b). A peculiar feature is the apparent encirclement of the free end of the posterior enamel plate by dentine.

M_3 is more elongate and narrower than the other molars, so that the two flexids are wider (especially at their open ends) than in the anterior molars. This is partly due to the lesser amount of wear on this tooth. The enamel has only just been interrupted on the anterior face of the tooth, but is broadly absent on the lingual face of the talonid. The lingual side of the tooth is grooved, as in M_2, but the mesoflexid does not seem to be dammed. This is not certain, however, due to the cement filling. The hypoflexid contains little cement, and is not dammed except at the very base of the crown, where there is a prominent cuspule. The absence of cement here is very possibly due to its removal during preparation.

Loomis' statement (1914, p. 193) that the folds are narrowest at the margin of the teeth and expand toward the center is true of the mesoflexids, due to their having been dammed by the cingular outgrowths of the trigonid and talonid, but is definitely not true of the hypoflexids.

A section of the right lower incisor is associated with this specimen as well as a fragment of the mandible. The tooth is egg-shaped in cross section, with a round, wide, enamel-covered anterior face and a tapering posterior side (Fig. 23B). The lingual margin is nearly straight. The enamel extends about a third of the way around the lateral surface and about a fifth of the distance around the lingual face. The enamel is smooth, and is rather thin. The pulp cavity is very small and is essentially circular near the tip of the tooth. The tooth is quite long, with a large radius of curvature.

The affinities of *Litodontomys* appear to be with the Dasyproctidae, but its position within the family is uncertain. There are some similarities to *Cephalomys* in the cheek teeth and in the incisor, and also in crown height and the tendency toward nondeposition of enamel, but there are also differences. The premolar outlines are very different, for example, and *Cephalomys* lacks cement. There are resemblances to the type material of *Olenopsis*[21] that may indicate some degree of relationship. P_4 of *O. uncinus* agrees in general outline, and, what is more important, in the presence of cement at the base of the crown and in the hypoflexid. The mesoflexid has been converted into a mesofossettid, very possibly in much the same manner as in *Litodontomys.* It is not likely that the two forms stood in an ancestor-descendant relationship. *Olenopsis uncinus* has a more

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[21] The type species, *O. uncinus* Ameghino from the Santa Cruz, was based on three syntypes: M.A.C.N. no. A 17, a fragmentary left mandible with the base of I, dm_4-M_2 (M_2 unerupted); M.A.C.N. no. A 1613, an isolated RP_4; and M.A.C.N. no. A 1614, an isolated Ldm^4 (Ameghino 1889, pp. 145-146. Pl. 6, figs. 14-16). M.A.C.N. no. A 17 is unfortunately not to be found in the Ameghino Collection. M.A.C.N. no. A 1613 has a deposit of cement. M.A.C.N. no. A 1614 lacks all trace of this substance and agrees very closely with dm^4 of *Neoreomys*, to which it may well be referable. Fields (1957, p. 325), in his description of the material he identifies as *Olenopsis aequatorialis* and places in the Dinomyidae, states that there is no evidence of cement in the teeth of that form, which raises the question as to whether or not this species is correctly referable to *Olenopsis.*

persistent crown pattern and the enamel was more extensive and differently distributed. In addition to the metafossettid, there are three small anterior fossettids, possibly remnants of a large anterior fossettid with an irregular floor or with spurs of enamel projecting into it, and a long, narrow metafossettid. The enamel extends down to the roots everywhere except along the posterior two-thirds of the lingual face, whereas in *Litodontomys* it is incomplete anteriorly as well. The two genera may or may not have had a common, pre-Deseadan ancestry, but the resemblances between them at least suggest some degree of affinity. There are no particular resemblances between *Litodontomys* and the material Fields described as *Olenopsis aequatorialis*.

TABLE 7

Tooth measurements (in mm.) of *Litodontomys chubutensis*, A.C.M. no. 3086

P_4	anteroposterior	3.21	M_2	anteroposterior	2.21
	width, metalophid	1.21*		width, metalophid	2.08*
	width, hypolophid	1.90*		width, hypolophid	2.03*
M_1	anteroposterior	1.97	M_3	anteroposterior	2.27
	width, metalophid	1.85*		width, metalophid	1.71*
	width, hypolophid	2.09*		width, hypolophid	1.59*
I_1	anteroposterior	1.88			
	transverse	1.44			

?DASYPROCTIDAE gen. et sp. indet.

Fig. 24

M.A.C.N. no. A 52-113, an isolated, unworn upper cheek tooth, presumably from Cabeza Blanca, Chubut.

This tooth shows a very high degree of unilateral hypsodonty, comparable to that of *Cephalomys*. It differs from that genus and from *Litodontomys* in the distribution of the enamel, which persists evenly all around the tooth as far as the beginning of the roots. Fields' figures of the Colombian material referred by him to *Scleromys* suggest a similar distribution of enamel (Fields, 1957, Figs. 10, 14). The protocone and hypocone are approximately subequal and sharply angulate internally. They are separated by a prominent hypoflexus that progressively diminishes and disappears about half way down the crown. The protocone-anteroloph crest curves forward and outward, losing altitude progressively, so that the extremity is far below the level of the apex of the paracone. The paraflexus deepens lingually, and would convert to a long, narrow parafossette. Protoloph and mure form a curving crest connecting the paracone and hypocone. Opposite the protocone, there is a short blunt projection that, with wear, would unite the two crests at this point. The paracone is joined to the external part of the posteroloph by a gently curving crest that bears two minute cuspular elevations. Protoloph, mure, posteroloph and this external crest isolate a large, deep fossette. From the external crest, opposite the second cuspular elevation, a prominent spur projects into this valley.

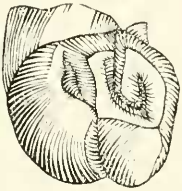

Fig. 24. ?Dasyproctidae, gen. et sp. indet. Left upper cheek tooth, M.A.C.N. no. A 52-113, x 6.

A slight swelling is present on the outer surface of the mure. The region of the hypocone is the highest part of the unworn crown. No trace of cement is present.

We are in some doubt as to whether this tooth should be interpreted as P^4 or as a molar. It agrees in outline with P^4 of Santacruzian *Scleromys* as figured by Scott, but not with Fields' (1957) referred material. It differs from both in the presence of the large spur in the posterior valley. This structure appears to be a remnant of a metaloph, the swelling on the mure representing the aborted inner end of the crest. So molariform a premolar would be decidedly exceptional in the Deseadan. If the spur and swelling be regarded as a metaloph in process of formation, then such a mode of origin would be exceptional for P^4 among caviomorphs. Agreement with the upper molars of Santacruzian *Scleromys* is close. These teeth lack the metaloph entirely, and, since this is clearly a secondary condition, the structure in M.A.C.N. no. A 52-113 could be regarded as indicating a molar in process of losing this crest. This we believe to be the more likely interpretation. It is supported by the structure of the only known Colhuehuapian dasyproctid, also an isolated upper molar (M.A.C.N. no. A 52-163),[22] in which the metaloph is interrupted by a deep notch in its outer half.

We believe that this specimen is probably a dasyproctid. It is clearly distinct from *Cephalomys* and there is no basis for reference to *Litodontomys.* As regards the even distribution of enamel on the crown, it is more normal, with respect to the later members of the family, than either of its contemporaries. The tendency toward loss of the metaloph suggests affinities with the Santacruzian *Scleromys* rather than with *Neoreomys,* in which complete loss of this crest occurs only on M^3, where it is represented merely by a small metacone behind the paracone (Scott, 1905, Pl. 65, figs. 1-2). M.A.C.N. no. A 52-113 shows no indication of a neoloph, however. This structure does occur in the Santacruzian *Scleromys,* as is revealed by a minute remnant of the floor of the neofossette in M^1 of M.A.C.N. no. A 10142 and by the presence of a neofossette in M^3 of M.A.C.N. no. A 4361. (The isolated Colhuehuapian molar, in which the neoloph and neofossette are fully developed and the metaloph is in process of reduction, demonstrates that these are neofossettes and not metafossettes.) If M.A.C.N. no. A 52-113 was in the ancestral line leading to the Santacruzian *Scleromys,* then a neoloph must have arisen in post-Deseadan time. This is conceivable, but more and better material is clearly needed before any conclusion can be reached.

TABLE 8

Tooth measurements (in mm.) of M.A.C.N. no. A 52-113

Anteroposterior	3.10†
Greatest width	3.83†
Height, buccal side	2.80
Height, lingual side	over 6.4

† = Greatest extra-alveolar diameter.

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[22] This tooth is one of Ameghino's two syntypes of *Luantus initialis* (see below, p. 365).

Superfamily CAVIOIDEA L. Kraglievich 1930

Family EOCARDIIDAE Ameghino 1891

Two cavioid genera, *Asteromys* Ameghino and *Chubutomys* gen. nov., that differ rather strikingly from each other, occur in the Deseadan. So different are they that we once thought that *Chubutomys* should be considered as an aberrant dasyproctid. Study of the Colhuehuapian and Santacruzian material in the Ameghino Collection, however, has revealed that there are two clear-cut groups within the Eocardiidae, one typified by *Luantus,*[23] the other by *Eocardia* and *Schistomys. Asteromys* is clearly referable to the first of these, and *Chubutomys* is as certainly an early representative of the second; both these genera possess small, ephemeral mesofossetids, a typical eocardiid character. The two groups may be distinguished as follows:

LUANTINAE subfam. nov. Cheek teeth mesodont to hypsodont; hypoflexus and hypoflexid extending approximately half way across crowns; external fossettes and internal fossettids relatively persistent; metalophid lost on M_{2-3} of later forms; enamel extending equally far down all sides of cheek teeth; no cement.

Distribution. Deseadan to Santacruzian, Patagonia.

Genera. Asteromys Ameghino 1897, Deseadan; *Luantus* Ameghino 1899, Colhuehuapian to Santacruzian.

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[23] Ameghino, subsequent to his description of the Colhuehuapian *L. initialis* (1902c, pp. 114-115), consistently referred *Luantus* to the Capromyidae (Myocastoridae of his usage). *L. initialis* was based on two syntypes, a portion of a left ramus with the base of the incisor and P_4-M_2 (M.A.C.N. no. A 52-164), and an isolated right upper molar (M.A.C.N. no. A 52-163) — not a premolar, as he supposed. The latter represents a hitherto unknown dasyproctid and as such has been briefly referred to above (p. 364), but it clearly has nothing to do with the jaw fragment, which we designate as the lectotype of the species. The two specimens were presumably picked up and packed together, a circumstance that Ameghino all too frequently considered to be sufficient proof of natural association. There is a general resemblance between the lower molars of the Santacruzian species of *Scleromys* and those of *Luantus,* but the latter retains the metalophid in M_1 and has a short, typically eocardiid incisor that does not extend back beyond M_2. Scott (1905, p. 388), evidently on the basis of the lectotype jaw, placed *Luantus* with *Eocardia* and *Schistomys,* an assignment followed by Simpson (1945, p. 94) and Landry (1957a, p. 43). There can be no doubt that this is the correct position of the genus, although we cannot agree with Landry that "a form only a little less specialized than *Luantus* . . . may have been the common ancestor of the Superfamilies Octodonoidea, Cavioidea, and possibly Chinchilloidea" (*op. cit.,* p. 44). The Deseadan *Asteromys* is such a less specialized form, and it is unmistakably a cavioid. Schaub *(in* Stehlin and Schaub 1951, p. 369) considers that *Luantus* is widely separated from the Eocardiidae, and should be referred to the "Acaremyinae" (1953a, p. 399) because the second and third inner "synclinals" of the lower cheek teeth are united. This condition, which is due to loss of the metalophid in M_{2-3}, we cite as a character of the new subfamily Luantinae. We, too, regard it as a character of importance, though we cannot agree that it requires the removal of *Luantus* from the Eocardiidae.

EOCARDIINAE. Cheek teeth hypsodont to hypselodont; hypoflexus and hypoflexid, after slight wear, extending more than half way across crowns; external fossettes and internal fossettids becoming shallow and ephemeral; metalophid retained; enamel of crowns not extending equally far down all sides of cheek teeth, and lacking, after slight wear, on external sides and antero- and posteroexternal corners of uppers, on internal sides and antero- and posterointernal corners of lowers; cement present in some later forms on sides of crowns and in hypoflexus and hypoflexid.

Distribution. Deseadan to Santacruzian, Patagonia.

Genera. Chubutomys gen. nov., Deseadan; *Eocardia, Schistomys, Phanomys*[24] Ameghino 1887, Santacruzian.

Both in the luantines and in the eocardiines with rooted teeth, the hypoflexus and hypoflexid decrease in extent toward the base of the crown and disappear entirely before the root is reached. The known luantines may well have formed a direct phyletic series. *Luantus* has not hitherto been recorded from the Santa Cruz proper, but there are from this horizon two good specimens, a right mandible (M.A.C.N. no. A 2018) and a palate (M.A.C.N. no. A 2025), and a number of isolated teeth in the Ameghino Collection that are certainly referable to the type species, *L. propheticus* Ameghino 1898.[25] The type specimen of this species was found in the Pinturas, or *Astrapothericulus*, beds, supposed by Ameghino to be older than the Santa Cruz. Examination of the scanty, and fragmentary, Pinturas fauna reveals, however, that there is really no good evidence for con-

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[24] This is a very poorly known genus. The syntypes of *P. mixtus,* the type species, are not now in the collections of the Museo de La Plata, and must be presumed lost. Material in the Ameghino Collection described later by Ameghino (1889, p. 217, Pl. 10, figs. 12-25) agrees well with the brief original description. Unfortunately, these "neosyntypes" (M.A.C.N. no. A 2022) are all isolated teeth, as are the syntypes of *P. vetulus* Ameghino (M.A.C.N. no. A 2024). The best specimen *of P. mixtus,* the maxillary fragment with P4-M2 figured in 1889 (Pl. 10, fig. 21) and in 1906 (Fig. 313), cannot be found in the collection. The available material shows that *Phanomys* is a valid form with rooted molars but with cement; hypoflexid and distribution of enamel are as in *Eocardia* and *Schistomys. Hedymys,* also described by Ameghino in 1887, is a *nomen vanum* (see below).

[25] P_4 and M_3 of M.A.C.N. no. A 2018 are so similar to the types of Ameghino's *Eocardia prisca* and *Luantus propheticus* as to show that these species were based on RM_3 and RP_4, respectively, of one species, perhaps even of one individual. The former has line priority, which we disregard. *Luantus propheticus* was described by Ameghino as the type species of the genus, and the fact that *Eocardia prisca* was described two lines above would have been an altogether inadequate reason for violating common sense and presenting a new combination. *B. prisca* is here relegated to the synonymy of *L. propheticus.*

sidering it to be anything but a Santacruzian local fauna. The palate, M.A.C.N. no. A 2025, a young specimen with dm^4-M^3 preserved, reveals a very interesting feature of *Luantus* that must be recorded here. M^2 has a swelling in the center of the posteroloph, which on M^3 becomes a minute fossette, partially open posteriorly on the left side. This is a rudimentary neofossette, the first stage in the formation of a neoloph such as occurs in various caviomorphs and it is of the greatest interest to find a tendency toward this condition occurring in the family. This specimen has been figured by Scott (1905, Pl. 68, fig. 27) and by Ameghino (1906, Fig. 311, p. 419). The former figure is very inaccurate, and shows neither the swelling nor the minute fossette; the latter shows the swelling but not the minute fossette and errs in depicting the enamel as missing from the outer face of M^1. Scott called the specimen "*Eocardia* sp. (referred to *Hedymys integrus*)" while Ameghino labeled it "*Hedimys integrus*," and thereby hangs another lengthy footnote.[26]

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[26] *Hedymys integrus* (Ameghino, 1887, p. 14; 1889, pp. 217-218 — the unjustified emendation to *Hedimys* dates from 1894, p. 331) was based on a single upper molar, measuring 3 mm. in length and breadth, with a large internal and two small external roots, a deep hypoflexus and no enamel on the external face. The tooth was evidently only moderately worn since it measured 6 mm. high on the internal side and 4 mm. on the external. The type is not now in the Museo de La Plata and is almost certainly lost. From the description, it is clear that the specimen was an eocardiine, but beyond that it is impossible to go. *Hedymys integrus* Ameghino 1887 is a *nomen vanum* in the fullest sense of that useful term. Scott (1905, p. 472) stated that in his opinion the type was a milk molar of *Eocardia*, but there is no real evidence for this view. In the Ameghino Collection, however, the palate, M.A.C.N. no. A 2025 is labeled as "*Hedimys integrus* tipo." This label, and others like it purporting to identify the types of species described in 1887, has an interesting history. After Ameghino's resignation from the staff of the Museo de La Plata in 1888, he was denied access to the collections by Moreno, the Director. Consequently, he had no opportunity to compare Santacruzian specimens obtained at a later date with those he had described in his paper of 1887. It then became his custom to label as types (and his concept of a type was not that now current) specimens in his own collection that he had referred, without benefit of direct comparison, to species described in that publication, frequently selecting material figured in his great work of 1889. The present specimen was not there figured, and it is difficult to understand why he made the identification, because the teeth considerably exceed the measurements he gave for *H. integrus*. How thoroughly Ameghino had come to base his conception of *Hedymys* on this newly established "type" is shown by his subsequent description of "*Hedimys*" *gracilis* (1906, Fig. 312, p. 420 — the figure caption is the only mention in his writings of this species although it is not there stated to be new). "*H.*" *gracilis* was based on two isolated cheek teeth, M.A.C.N. no. A 4481, an upper molar (designated P^4 by Ameghino) and dm$_4$. The upper molar is here designated as the lectotype; the dm$_4$ is probably referable to *Eocardia*. The molar is smaller than any of the cheek teeth of the new "type" of *H. integrus* and agrees with them in pattern, allowing for the difference in wear, but the measurements (L. 3.0, W. 2.5 mm.) do not suffice to separate it from the real type (now lost) of *H. integrus*. The degree of wear is almost exactly the same as in this lost specimen (external height 6.0, internal 3.3 mm.), however, and this reveals that "*H.*" *gracilis* is not *H. integrus*, since Ameghino's description of the latter stresses the absence of enamel on the outer face and makes no mention of fossettes on the grinding surface, whereas there is enamel and there are fossettes on the lectotype of *gracilis*. The species must be listed as *Luantus gracilis* Ameghino.

The absence of eocardiines in the Colhuehuapian is certainly an accident of collecting; the family is very rare prior to the Santa Cruz, being represented by only three identifiable specimens from the earlier deposits. The Colhuehuapian *Archaeocardia* is not an eocardiid. The two proposed species, "*Palaeocardia*" *mater* Ameghino 1902c and *Archaeocardia mustersiana* Ameghino 1904, both fall into the synonymy of the echimyid *Protacaremys prior* Ameghino 1902 (Patterson and Kraglievich ms.). Simpson (1945, p. 94) inadvertently credits *Archaeocardia* to Ameghino. The name was proposed by Cossmann in 1902[27] to replace *Palaeocardia* Ameghino 1902 *nec* Hall 1867. The hypselodont *Eocardia* and *Schistomys*, both adequately known from Scott's work, are the only common eocardiids. Both forms, and also the rooted *Phanomys*, may well have been derived from *Chubutomys*. The phylogeny of the family may be tentatively expressed as shown in Figure 25.

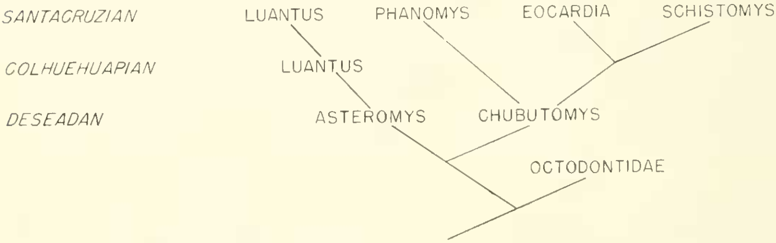

Fig. 25. Tentative phylogeny of the Eocardiidae.

Subfamily LUANTINAE

Asteromys Ameghino

Asteromys Ameghino, 1897c, p. 495; 1898, p. 176. Loomis, 1914, pp. 194-195 (in part). Stehlin and Schaub, 1951, p. 244.

Type species. A. punctus Ameghino, 1897.

Distribution. Deseadan, Patagonia.

Emended diagnosis. Cheek teeth mesodont, considerably lower-crowned than in *Luantus initialis*; P_4 not molariform, anterior

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[27] In an unsigned footnote on page 176 of the Revue Critique de Paléozoologie, sixième année.

face with deep vertical groove, minute fossettid on side of ectolophid, mesoflexid large, widely open internally; metalophid present on molars; M_{2-3} not notably larger than P_4-M_1.

ASTEROMYS PUNCTUS Ameghino
Fig. 26

A. punctus Ameghino, 1897c, p. 495; 1906, p. 412, Fig. 287. Stehlin and Schaub, 1951, Fig. 390, p. 244.

Type. M.A.C.N. no. A 52-110, fragment of right ramus with base of I, P_4-M_3, part of anterior root of dm_4.

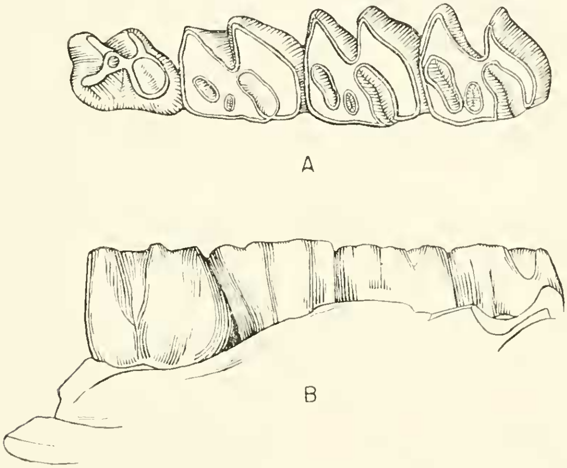

Fig. 26. *Asteromys punctus* Ameghino. RP_4-M_3, type, M.A.C.N. no. A 52-110. *A*, crown, *B*, labial view, x 5.

Hypodigm. Type only.

Horizon and locality. Deseado formation; evidently Cabeza Blanca, Chubut.

Diagnosis. As for the genus; for tooth measurements see Table 9.

The cheek teeth are moderately high-crowned and exhibit a strong degree of unilateral hypsodonty. The enamel is continuous all around the crowns. P_4 differs somewhat from those of other Deseadan rodents. It is less curved and hence exhibits a lesser degree of unilateral hypsodonty than the molars. The crown tapers toward the apex both transversely and anteroposteriorly; the maximum area of grinding surface would not be attained until wear had proceeded about half way down the crown. The upper portion of M_1 curves forward over the obliquely sloping upper part of the posterior face of the premolar, so that with wear the relative proportions of the two teeth would change considerably (Fig. 26). The talonid of P_4 is essentially molariform, the only difference being that the metaflexid is shallower; the hypolophid arises near the center of the tooth and is directed slightly posteriorly, thus suggesting that it may have arisen anterior to the primary posterior crest as in the specimen of *Sciamys* referred to above (p. 297). The trigonid is very different from that of the molars. The anterior face is deeply grooved and the groove extends back between the protoconid and metaconid, which thus appear as though situated at the ends of crests that diverge from the ectolophid. Immediately behind the point of divergence, there is a minute fossettid on the inner side of the ectolophid. The differences from the trigonid of P_4 of *Platypittamys* are striking but apparently not profound. The divergent crests running to the protoconid and metaconid appear to be merely the two wings of the anterolophid, here deeply concave due to the anterior groove, and the inner wall of the minute fossettid is best interpreted as a rudimentary metalophid connected, again due to the presence of the groove, to the metaconid wing of the anterolophid. The crown elements present in both thus appear to be comparable. In *Luantus*, the anterior groove has been eliminated, the short anterolophid is transverse and the metalophid is at first small and freely projecting (*L. initialis*), later becoming larger and uniting with the inner extremity of either the anterolophid or the hypolophid (*L. propheticus*). The hypoflexid extends about half way across the crown and persists nearly to the root. The mesoflexid is very large, wide above and tapering downward; it persists for about two-thirds of the height of the crown. The metaflexid is a mere nick in the rim of the shallow metafossettid basin.

The molars are very similar in size, a notable difference from *Luantus*, in which M_{2-3} are larger than P_4-M_1. The only apparent structural difference within the series is the greater depth of the metaflexid in M_3, which is not entirely due to the difference in wear. The protoconid and hypoconid form sharp external angles and the lingual border is very straight in all. The metalophid is present and complete on all molars, whereas in *Luantus initialis* it is interrupted on M_2 (M_3 unknown) and in *L. propheticus* absent on M_{2-3}. The hypoflexid extends approximately half way across the crown, diminishing in size and ending near the roots. The metaflexid is the deepest of the internal folds, and the others, if present at all, must have been ephemeral. The minute mesofossettid is the smallest and shallowest of the fossettids, as in all eocardiids. The parafossettid is considerably larger and somewhat deeper, and the metafossettid is the largest and deepest of the three. The metaconid is a large cusp and the metalophid unites with its posterior extremity. In *Luantus initialis*, the inner extremity of the metalophid appears to have lost its connection with the metaconid and to have become secondarily enlarged on M_2.

The incisor is small in comparison with the size of the cheek teeth, and there is not much difference between the two diameters. The anterior face is gently convex. The tooth lies ventromedial to the cheek tooth row, relatively lower than in later forms, and evidently did not extend posteriorly beyond M_2. The internal face of the horizontal ramus is gently shelving above the incisor, as in other eocardiids. The lateral surface of the mandible is not preserved in this specimen and is incomplete in the lectotype of the Colhuehuapian *Luantus initialis*. It is fortunately preserved in one of Ameghino's specimens of *L. propheticus*, which reveals a typically eocardiid structure.

Ameghino placed *Asteromys* in his family Cephalomyidae, which he regarded as broadly ancestral to all caviomorphs, and indeed to all rodents. In 1898, he shot very close to the mark with his statement that the genus ". . . parece ser el antecesor de los cavinos" (1898, p. 176). By 1906, however, he appears to have receded from this conclusion for we find him making comparisons between *Asteromys* and *Alactaga*. Later authors, misled by the upper cheek teeth erroneously referred to "*A. prospicuus*" by Loomis, have placed the genus in the Erethizontidae (as ''Acaremyinae''). There can be no doubt whatever that Ameghino's views of 1898 were very nearly correct; *Asteromys* is unquestionably the most primitive known cavioid. It is equally clearly a member of the Luantinae, and none of its known features would seem to bar it from the ancestry of *Luantus*.

The contemporary, and much higher-crowned, *Chubutomys* shows that the eocardiid dichotomy began in pre-Deseadan time, but it is nevertheless probable that in *Asteromys* we have a comparatively little-modified descendant from the common ancestry. The lower molars are of the usual, four-crested, early caviomorph type. Apart from the higher crowns and the reduction of the mesoflexid-mesofossettid, a striking familial character that was presumably established early in the history of the group, there is no important structural difference from the molars of *Platypittamys*. The premolar, as Wood (1949, p. 20) has pointed out, is advanced over that of *Platypittamys* in talonid structure, and is superficially different in the trigonid, as noted above. These differences appear to be relatively trivial. The premolars of Santacruzian octodontids, especially the lowers, were extraordinarily variable in superficial detail (Patterson and Kraglievich ms.). Within *Sciamys principalis*, P_4 may or may not possess a grooved anterior face and a mesolophid and a fossettid on the side of the ectolophid, the talonid may or may not be molariform, and all combinations of these characters occur at random. If earlier octodontids were similarly variable — and it may be noted that the premolars of the two known specimens of *Platypittamys* are far from being exactly similar — derivation of the ancestral eocardiids from an octodontoid stem is altogether likely.

As stated elsewhere in this paper, caviomorphs do not possess, nor were they derived from forms possessing, a mesolophid in the lower molars. The ''mesolophid'' of P_4 of certain specimens of *Sciamys principalis* was an independently acquired premolar character. It crops up as one of a number of variants resulting from the essentially random variation of the talonid crestlets, which differ in position and in attachments to each other and to the metaconid, protoconid and ectolophid.

TABLE 9
Tooth measurements (in mm.) of *Asteromys punctus*, M.A.C.N. no. A 52-110.

I_1	anteroposterior	1.52
	transverse	1.45
P_4	anteroposterior	3.50†
	transverse	2.51†
M_1	anteroposterior	2.97
	transverse	2.58†
M_2	anteroposterior	3.10
	transverse	2.77†
M_3	anteroposterior	3.17†
	transverse	2.30†

† = Greatest extra-alveolar diameter.

Subfamily EOCARDIINAE

CHUBUTOMYS gen. nov.

Type species. C. simpsoni sp. nov.

Distribution. Deseadan, Patagonia.

Diagnosis. Cheek teeth much higher-crowned than in *Asteromys,* approaching hypselodonty, higher than in *Cephalomys* and *Litodontomys;* lower molars with hypoflexids extending across approximately two-thirds of crown diameter; enamel interrupted after wear on anterior face and posterointernal corner of teeth, more persistent on internal sides than in later eocardiines; cement absent.

CHUBUTOMYS SIMPSONI[28] sp. nov.

Fig. 27

Type. A.M.N.H. no. 29557, fragment of left ramus with M_{2-3}.

Hypodigm. Type only.

Horizon and locality. Deseado formation; Cabeza Blanca, Chubut, Argentina.

Diagnosis. As for the genus; for tooth measurements see Table 10.

The teeth are very high-crowned. As in *Cephalomys,* the enamel extends to variable distances down the sides of the teeth,

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[28] Named for Dr. George Gaylord Simpson, leader of the Scarritt Patagonian Expeditions and finder of the type.

so that it is interrupted after wear on the anterior face (beginning at the lingual side) and at the posterointernal corner. The large hypoflexid, dividing the teeth into two equal halves, extends about two-thirds of the way across the crown. At the lower levels of the crown, this fold gradually becomes shallower, disappearing just above the roots, as in the luantines and in other eocardiines with rooted cheek teeth. The anterofossettid is a narrow oval, diagonally placed on the crown and extending well down into the tooth. On M_3, the posterior end of the metaflexid still opens lingually. On M_2, it had just been converted to a metafossettid, which also extends deep into the crown. No trace is present of the ephemeral mesofossettid, the smallest and shallowest of the folds in all eocardiids. The buccal tips of the protoconid and hypoconid are partially separated from the rest of the tooth by faint vertical furrows (Fig. 27), which Scott (1905, p. 462) observed in *Eocardia*, and which also occur, although not constantly, in *Luantus*.

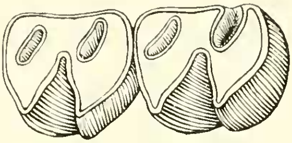

Fig. 27. *Chubutomys simpsoni* gen. et sp. nov. LM_{2-3}, type, A.M.N.H. no. 29557, x 5.

Enough of the bone is present on the lateral side of the ramus fragment to reveal the presence of a rather weak masseteric crest of eocardiid type.

There are several points of resemblance to *Scotamys*: the ephemeral nature of the lingual flexids; the linguad extension of the hypoflexid; and the disposition of the enamel. Among other features, however, the two genera differ in that the hypoflexid is shallower, the antero- and metafossettids persist longer, and there is no cement in *Chubutomys*. There are also resemblances to *Cephalomys* and *Litodontomys*, but the present form is more hypsodont and the crown is divided into two lobes by the hypoflexid instead of by that fold and the mesoflexid, which disappears quickly in *Chubutomys*. As in *Neoreomys*, the hypoflexid becomes progressively more anterior in position as the root is approached and the outline of the tooth becomes less elongate and more quadrangular.

These various similarities to other high-crowned caviomorphs are merely such as would be expected to occur among forms that had diverged from a common ancestry not long prior to the Deseadan. The several characters in which *Chubutomys* resembles the eocardiines seem definitely to indicate close affinity. The obviously small and ephemeral mesoflexid-mesofossettid, already worn away in the type specimen, the very high crowns, the very extensive hypoflexid, the general shape of the crowns, and the sharply angulate protoconids and hypoconids with their tendency toward constriction of the tips by faint vertical furrows — all these present a combination of characters typical of this subfamily. The distribution of enamel is more extensive internally than on the corners. The bearing of *Chubutomys* and other high-crowned Deseadan forms on the time of origin and initial radiation of the Caviomorpha is discussed in the concluding section.

TABLE 10

Tooth measurements (in mm.) of *Chubutomys simpsoni*, A.M.N.H. no. 29557.

M_1	anteroposterior	3.42
	width metalophid	2.65
	width hypolophid	2.80
M_2	anteroposterior	3.58
	width metalophid	2.73
	width hypolophid	2.65

EOCARDIIDAE gen. et sp. indet.

Fig. 28

A.C.M. no. 3054, RM^3, figured by Loomis (1914, Fig. 129) as M_2 of *Asteromys prospicuus* Ameghino. Cabeza Blanca, Chubut.

M.A.C.N. no. A 52-87, R dm^4 (the tooth, referred to above, p. 357, that was in the same box with the syntypes of "*Asteromys prospicuus*"). Presumably Cabeza Blanca, Chubut.

The Amherst specimen (Fig. 28) has a wear facet at only one end, showing that it cannot have been M$_2$, as Loomis supposed. There was a single internal root, indicating that the tooth is an upper. The lack of divergence of the roots and the rather high crown suggest that it is a permanent tooth. We consider it most probably to be M^3. The tooth is elongate, quite high-crowned, despite considerable wear, and shows marked unilateral hypsodonty. The parafossette is larger and deeper than either the mesofossette or the metafossette. Of the three, the mesofossette is the smallest and the metafossette is the shallowest, and hence the most ephemeral. There is a partial dam across the parafossette, so that it might be split into two fossettes briefly at the right stage of wear. These characters combine to suggest eocardiid affinities.

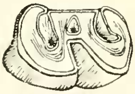

Fig. 28. Eocardiidae gen. et sp. indet. RM$^{3?}$, A.C.M. no. 3054, x 5.

M.A.C.N. no. A 52-87 lacks the posteroloph and is not quite complete externally. It is not as worn as the Amherst tooth — the paraflexus is still open — but is very similar in structure. There is also one large internal root and two small external ones. We suspect this tooth to be dm^4.

These two teeth certainly represent the same form. The fact that they agree with the lower molars of *Asteromys punctus* in possessing a similar complete investment of enamel inclines us to suspect that they may possibly be referable to that species. Certainty, of course, can only come with discovery of more complete material.

Table 11

Tooth measurements (in mm.) of Eocardiidae indet.

	A.C.M. no. 3054, RM^3	M.A.C.N. no. A 52-87, dm^4?
Anteroposterior	3.05	—
Width protoloph	1.70	1.91
Width metaloph	1.73	—

Superfamily ERETHIZONTOIDEA Simpson 1945
Family ERETHIZONTIDAE Thomas 1897
Subfamily ERETHIZONTINAE Thomas 1897

The New World porcupines are represented in the Deseadan by various isolated teeth that indicate the presence of one genus, *Protosteiromys* nov., with two species. These fragmentary remains reveal that the typical, rather simple molar pattern of the family was then already fully established; in this character there has been almost no subsequent change. The Recent erethizontids are rather distinct in their myology, serology and lice from the remaining caviomorphs, and there are considerable differences between the Santacruzian representatives of the family and other contemporary forms in the structure of the skull and the postcranial skeleton. The skull structure of the Colhuehuapian erethizontids, so far as known, is generally similar to that of the Santacruzian ones. It seems likely that the cranial and postcranial specializations characteristic of the family were already under way by Deseadan time. At the least, it would be unsafe to assume that the similarity in molar structure between the erethizontids and the earliest octodontids and echimyids indicated that the Erethizontidae had diverged from the ancestral stock only slightly prior to the Deseadan.

PROTOSTEIROMYS gen. nov.

Type species. Eosteiromys medianus Ameghino 1903.

Distribution. Deseadan, Patagonia.

Diagnosis. Molars lower-crowned than in later forms other than *Eosteiromys:* upper molars with four main crests, rudimentary neoloph; mesoflexus shallower than in *Eosteiromys;* hypocone on same anteroposterior line as protocone on M^{1-3}; lower molars with four crests, antero- and metafossettids nearly or fully formed.

The taxonomic history of this genus is rather confused. In 1901 Ameghino (pp. 76-78) gave a faunal list of the Santacruzian including *Steiromys principalis* and *S. annectens,* and indicated that the Coendidae (=Erethizontidae), to which he referred them, were present in the Colhué-Huapí (=*Colpodon* beds). The following year (1902c, p. 110), he described *Eosteiro-*

mys homogenidens, nov. gen., nov. sp., from the Colhué-Huapí, but marked it as having been mentioned in the 1901 paper, which was not the case. A year later (1903a, p. 129), Ameghino discussed *Eosteiromys homogenidens* and *E. uniformis* from the Colhué-Huapí, and *E. medianus* from the Deseado (=*Pyrotherium* beds). Although he did not describe *E. medianus* as new in this paper, his brief discussion and figure (Fig. 51) are sufficient to date the species from this paper. The next year (1904, p. 249), he formally described *E. medianus* as a new species from the Deseado, referring it with some doubt to the Colhuehuapian *Eosteiromys*, and cited his previous reference of 1903. This confusion was no fault of Ameghino's, but was the result of papers being published in different journals. Also in 1904, he described *Parasteiromys uniformis*, nov. gen., nov. sp., from the Colhué Huapí, referring back to the 1903 paper where he had figured and described it as *Eosteiromys uniformis*.

In view of this rather confused situation some comment on the Colhuehuapian erethizontids is necessary. Three genera have been recorded: *Eosteiromys*, *Parasteiromys* and *Steiromys*. The first of these is a relatively primitive form, but little advanced over *Protosteiromys*, and with a non-molariform P^4. *Parasteiromys* was originally diagnosed by possession of P^3, reduction of the mure (resulting in continuity of the meso- and hypoflexus), and the presence of a neofossette. The type specimen of *P. uniformis* is a very young individual in which dm^4-M^1 are preserved, not P^4-M^1 as Ameghino supposed. The evidence for a tooth anterior to dm^4 consists of the perforations in the maxilla shown in his figure and interpreted as alveoli (1903a, pp. 126-7, Fig. 47). At the same time, he stated that a fifth upper cheek tooth also occurred in young individuals of *Steiromys detentus*, presumably on similar evidence. Whatever these perforations may be, and they are probably vascular, they are not alveoli. Similar ones occur in young Recent erethizontids and in these no cheek tooth anterior to dm^4 is ever present. A neofossette occurs in several erethizontids, and is fully as well developed in the Santacruzian *Steiromys duplicatus* as it is in the type of *P. uniformis*. The reduction of the mure scarcely seems to be a character of generic significance, and we therefore refer *uniformis* to *Steiromys*. The species *Steiromys axiculus, S. tab-*

ulatus and *S. nectus,* the last two synonyms of the first, represent a new and very distinct genus, *Hypsosteiromys* (Patterson, 1958a), also with a non-molariform P^4.

The Deseadan species, *medianus,* is generically distinct from the forms from the Colhué-Huapí. Direct comparison with the type of *E. homogenidens* reveals that the latter has a considerably deeper mesoflexus, and a hypocone more external in position on $M^{1\text{-}2}$. We therefore have no alternative but to propose a generic name and have selected *Protosteiromys.* A second, and more primitive species, *P. asmodeophilus,* is described below.

This genus may be characterized as including very low-crowned erethizontids with the four principal crests of the upper molars usually still quite distinct and with incipient division of the posteroloph to form a neoloph. In the lower molars, the fossettids are already nearly or quite formed. Variability in homologous teeth is considerable, as in later forms, which warns against too rigid a reliance on diagnoses based on one or two specimens.

The upper premolar is unfortunately unknown, but there is no reason to doubt that only three crests, the anteroloph, protoloph, and posteroloph, were present. This tooth is not yet molariform in the Colhuehuapian *Eosteiromys homogenidens,* in which a small fossette in the posteroloph marks the rudiment of a fourth crest.

Five isolated upper molars are known: Ameghino's type of *medianus*; A.C.M. no. 3014, described by Loomis (1914); and three specimens in the Muséum National d'Histoire Naturelle. All are referred to *P. medianus.* The type upper molar, $M^{1\,\mathrm{or}\,2}$ (Fig. 30A), is a little wider than long, and shows a slight degree of unilateral hypsodonty; there is a wear facet at each end. The protocone and anteroloph form a curving, lunate, crest that extends almost to the paracone, only a very shallow paraflexus intervening. The protocone is connected to the anterior end of the short mure by a well developed isthmus, the protoloph continuing externally from this point in a very gentle curve, convex forward. A slight terminal swelling marks the position of the paracone. The thin, straight and nearly transverse metaloph arises at the posterior end of the mure, both loph and mure diverging from the anterior arm of the hypocone. A very shallow metaflexus intervenes between the metaloph and the anteriorly curving external extremity of the posteroloph. Both para- and metaflexus would be converted to fossettes with very little additional wear. The mesoflexus is deeper and it is doubtful if a mesofossette would ever have developed. All three flexi are rather shallow relative to the height of the crown. The protocone is moderately elongate anteroposteriorly, more so than in most erethizontids. Probably in correlation with this, the hypocone is decidedly internal in position, on the same anteroposterior line as the protocone. Posterointernally, it is produced into a thin, prominent crest. The hypoflexus is widely open in the unworn or little worn crown but rapidly decreases in size upward, due to the forward slope of the anterior face of the hypocone. It extends for approximately half the height of the internal face of the tooth. On the anterior slope of the external half of the posteroloph there is a small, fifth crest, the neoloph, which has isolated, with the posteroloph, two small neofossettes, a minute external one and a slightly larger internal one. This crest is further discussed below (p. 391).

The other first or second molars (Fig. 30B) differ from the type, and among themselves, in a few respects. Only one small neofossette is isolated by the posteroloph and the neoloph, the anteroloph may be less curved and the paraflexus and metaflexus slightly deeper. If we may judge from *Steiromys,* in which the molars show a considerable degree of variability in these features, such minor differences have no taxonomic significance.

The last molar is represented by M.N.H.N. no. 1903-3-15, (Fig. 30C), a practically unworn specimen. As in M^3 of all erethizontids, the hypocone is more buccad in position than the protocone. The protocone is not united with the protoloph; spurs from the protocone and the lingual end of the protoloph approach each other but would not have united until a considerably more advanced stage of wear had been reached. This feature also occurs in some specimens of *Hypsosteiromys,* and may crop up in molars of *Steiromys* and the Recent forms. Anteroloph and protoloph are united buccad, an advanced feature not found in the other specimens. The metaloph is not connected to the hypocone. The neoloph is rudimentary and the neofossette very small.

Five lower molars (Figs. 31, 32) are also known, of which three are of appropriate size for *P. medianus* and are accordingly referred to that species. The remaining two, which differ from the rest in large size, relative narrowness and other features, constitute the hypodigm of *P. asmodeophilus* described below. As in later erethizontids, the lower molars are relatively broad compared to their length. The four lophids are very distinct, stout and narrowing rapidly toward their summits, as are those of the upper molars. When unworn they tend to have a delicate appearance, which is rapidly lost with wear. The cusps are almost indistinguishable from the crests, only a few traces remaining in *P. medianus.* The hypolophid and posterolophid are united lingually to isolate the metafossettid, even in unworn teeth. The anterofossettid is similarly isolated in the type of *P. asmodeophilus;* in the other available teeth a slight and shallow notch intervenes between the anterolophid and metalophid. The mesoflexid is the deepest of the lingual folds. Only after great wear, if at all, would a mesofossettid be formed. The hypoflexid is deeper than the mesoflexid and extends into the crown surface for slightly over a third of the total width of the tooth. A thin, prominent spur extends anteroexternally from the site of the hypoconid, but, in contrast to some later forms, there is no corresponding spur from the site of the protoconid. There is no trace in the anterofossettid of any cuspules or crestlets, such as may occur in later forms (cf. *Steiromys duplicatus,* Scott, 1905, Pl. 66, fig. 2a).

The upper and lower molars of this earliest known erethizontid genus show no particular resemblance to those of the Hystricidae, in which the unworn crowns have massive, tuberculate and closely appressed crests (Friant, 1935, p. 231).

Protosteiromys seems clearly to be related to *Eosteiromys* of the Colhuehuapian and to *Steiromys* of the Colhuehuapian and Santacruzian, to which it may well have been directly ancestral. The Colhuehuapian *Hypsosteiromys* is sufficiently specialized to suggest that its ancestry may have been distinct in the Deseadan. The only known later Tertiary form is the relatively gigantic *Neosteiromys bombifrons* Rovereto from the Pliocene of Catamarca, the largest known erethizontid (condylobasal length 151 mm.); this was probably a descendant of *Steiromys.* The living erethizontids appear readily derivable from an ancestor such as *Protosteiromys.* This form, then, as far as known, may be considered as representing essentially the basal stock of the Erethizontidae, as indicated in the phylogenetic chart of the Oligocene and Miocene members of the family (Fig. 29).

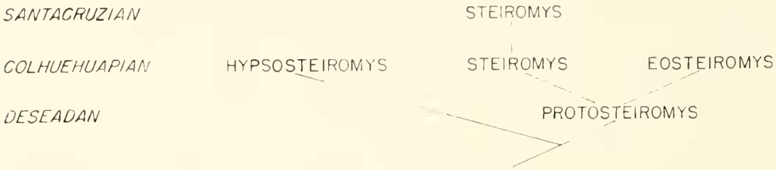

Fig. 29. Tentative phylogeny of the Oligocene and early Miocene Erethizontidae.

PROTOSTEIROMYS MEDIANUS (Ameghino)
Figs. 30-31

?*Eosteiromys medianus* Ameghino, 1903a, Fig. 51[29], p. 129.

Eosteiromys medianus Ameghino, 1904, p. 249; 1906, p. 413, Fig. 288; Loomis, 1914, p. 196, Fig. 130; Schaub, *in* Stehlin and Schaub, 1951, pp. 40-41, Fig. 38.

Type. M.A.C.N. no. A 52-111, RM$^{1 \text{ or } 2}$.

Hypodigm. Type and the following specimens: A.C.M. no. 3014, LM$^{1 \text{ or } 2}$ (*not* right, as Loomis stated); M.N.H.N. nos. 1903-3-83, LM$^{1 \text{ or } 2}$; 1903-3-84, broken LM$^{1 \text{ or } 2}$; 1903-3-15, unworn LM^{3}; 1903-3-16, LM$_{1 \text{ or } 2}$; 1903-3-17, RM$_{1 \text{ or } 2}$; 1903-3-85, RM$_{1 \text{ or } 2}$.

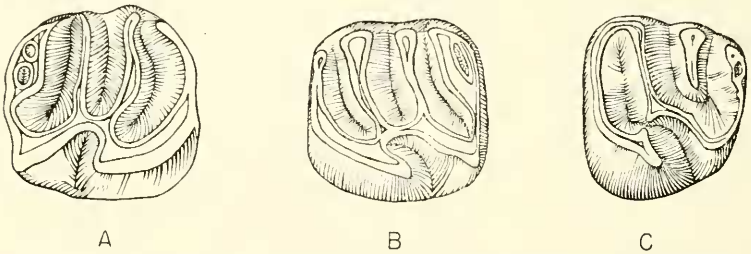

Fig. 30. *Protosteiromys medianus* (Ameghino). Upper molar teeth x 5. *A*, RM^{1}, type, M.A.C.N. no. A 52-111; *B*, LM$^{1 \text{ or } 2}$, A.C.M. no. 3014; *C*, LM^{3}, M.N.H.N. no. 1903-3-15.

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[29] Ameghino's figure is actually about four times natural size, and not three times as stated. It is inaccurate as regards shape and in showing one fossette too many at the rear of the tooth. Loomis' figure of A.C.M. no. 3014 is likewise inaccurate in shape and in most details of crown structure.

Horizon and localities. Deseado formation; the Amherst specimen is from Cabeza Blanca, Chubut; the Muséum National d'Histoire Naturelle specimens are from La Flecha, Santa Cruz. Ameghino (1904, p. 249) stated that the type was from the "pyrotheriense del Deseado." This was the Ameghinos' designation, variously written as "Deseado," "Río Deseado" or "Sur del Deseado," for the La Flecha locality.

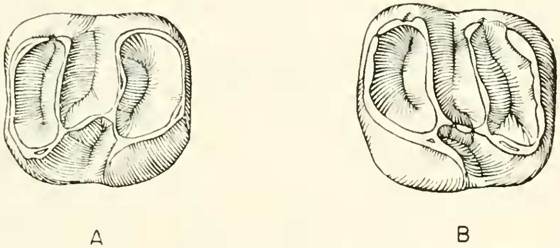

Fig. 31. *Protosteiromys medianus* (Ameghino). Lower molar teeth x 5. *A*, LM_1, M.N.H.N. no. 1903-3-16; *B*, RM_2, M.N.H.N. 1903-3-17.

Diagnosis. Smaller and relatively slightly higher-crowned than *P. asmodeophilus* (Table 12); lower molars shorter relative to width, fossettids thus more compressed anteroposteriorly, metalophid and hypolophid slightly convergent buccad.

PROTOSTEIROMYS ASMODEOPHILUS[30] sp. nov.
Fig. 32

Type. C.N.H.M. no. 15061, $RM_{1\ \mathrm{or}\ 2}$.

Hypodigm. Type and M.N.H.N. no. 1903-3-18, a worn and broken tooth, perhaps RM_3.

Horizon and locality. Deseado formation, La Flecha, Santa Cruz.

Diagnosis. Larger than *P. medianus* (Table 12); crowns of same actual height as in *P. medianus* and hence proportionately lower; fossettids, particularly the metafossettid, rounder and less compressed anteroposteriorly; mesoflexid with sides slightly divergent rather than slightly convergent lingually, lingual ex-

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[30] The type was found in the laboratory in matrix surrounding a femur of *Asmodeus osborni* Ameghino.

tremity deeper; central portion of ectolophid less oblique; no trace of distinct cusps.

In every character except the complete incorporation of the cusps into the crests, this species is more primitive than *P. medianus*. An early trend in dental evolution in the Erethizontidae was toward rather wide lower molars. Nearly every point in which *P. asmodeophilus* differs from *P. medianus* reflects a tooth that is relatively narrower in this diameter.

TABLE 12

Tooth measurements (in mm.) of *Protosteiromys*

P. medianus

	Type M.A.C.N. no. A 52-111 RM^1 or ^{2}	A.C.M. no. 3014 LM^1 or ^{2}	M.N.H.N. no. 1903-3-83 LM^1 or ^{2}	M.N.H.N. no. 1903-3-15 LM^3	M.N.H.N. no. 1903-3-84 LM^1 or ^{2}
anteroposterior	5.21	4.70*	4.48*	4.25*	ca. 4.63
width protoloph	5.48	5.00*	5.07*	4.81*	
width metaloph		4.75*	4.92*	4.09*	
height of crown, protocone	3.01	2.80	worn	2.77	

	M.N.H.N. no. 1903-3-16 LM$_1$ or $_2$	M.N.H.N. no. 1903-3-85 RM$_1$ or $_2$	M.N.H.N. no. 1903-3-17 RM$_1$ or $_2$
anteroposterior	4.88*	5.19*	5.18*
width trigonid	4.51*	4.62*	4.62*
width talonid	4.58*	4.84*	4.93*
height of crown, protoconid	2.47	worn	2.44

P. asmodeophilus

	Type C.N.H.M. no. P 15061 RM$_1$ or$_2$	M.N.H.N. no. 1903-3-18 RM$_3$?
anteroposterior	6.75*	ca. 7.20
width trigonid	5.52*	ca. 4.45
width talonid	5.60*	5.01*
height of crown, protoconid	2.50 (unworn)	2.47 (worn)

The referred specimen is somewhat narrower than the type. As in M_3 of *Hypsosteiromys*, the trigonid is appreciably narrower than the talonid, which is the chief reason for identifying this tooth as M_3, since the break at the rear of the tooth makes it impossible to determine whether or not there was a wear facet there. The anterofossettid is still a little open lingually, in contrast to the closed condition in the type.

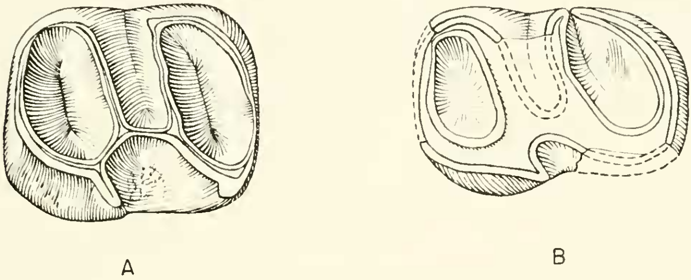

Fig. 32. *Protosteiromys asmodeophilus* sp. nov. Lower molar teeth x 5. *A*, $RM_{1 \text{ or } 2}$, type, C.N.H.M. no. P 15061; *B*, RM_3, M.N.H.N. no. 1903-3-18.

CAVIOMORPHA indet.

A single left lower molar (A.C.M. no. 3039, Cabeza Blanca, Chubut) cannot be allocated to any of the described forms. It is high-crowned but rooted, comparable to *Cephalomys* and *Litodontomys* and of about the same size as *L. chubutensis* and

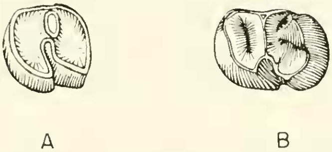

Fig. 33. Caviomorpha, gen. et sp. indet. x 5. *A*, left lower molar, A.C.M. no. 3039; *B*, $LM^{3?}$, M.N.H.N. no. 1903-3-21.

C. plexus. It does not have any cement, and the enamel is continuous around the crown almost, if not quite, to the roots. There is a hypoflexid that extends about half way across the crown, buccal to which is a small mesofossettid (Fig. 33A). Neither antero- nor metafossettid is present. This form is clearly distinct from all described species in the uniform extension of enamel and the persistence of the mesofossettid. It shows some resemblance to the tooth described above (p. 362) as Dasyproctidae indet., to which it may conceivably be related.

An isolated upper molar (M.N.H.N. no. 1903-3-21, La Flecha, Santa Cruz; Fig. 33B) appears to represent still a different structural type. There are three transverse crests, although a small anteriorly directed crestlet from the posteroexternal corner suggests the last remnant of a metaloph. There is a continuous ridge of enamel around the margin of the tooth, so that the buccal valleys were fossettes from the start. In the reduction to three crests, this tooth is reminiscent of the lower molars of *Deseadomys,* but no such reduction occurs in the uppers referred to that form. In addition, the present tooth is much too high-crowned to be referred to the Echimyidae. It is possible that the animal represented by this molar may also be a dasyproctid. The degree of hypsodonty is also comparable to that occurring in *Cephalomys* and *Litodontomys,* and the absence of a metaloph and the presence and direction of the short spur running from the metacone are reminiscent of conditions in the unworn upper molar of *Cephalomys plexus* (cf. Fig. 15A). There is a slight elevation near the middle of the posteroloph and another posterointernal to the protoloph on the mure. These two elevations occupy positions comparable to those occupied by the two ends of the neoloph in *C. plexus.*

It is obviously inadvisable to name either of these forms until material is available that would permit their relationships to be better understood. They clearly show how very far we are from a complete knowledge of the Deseadan rodents.

TABLE 13

Tooth measurements (in mm.) of Caviomorpha, indet.

	M.N.H.N. no. 1903-3-21 LM^3?	A.C.M. no. 3039 $RM_{1 \text{ or } 2}$
anteroposterior	2.75*	2.06
anterior width	2.10*	1.91*
posterior width	2.00*	1.94*

DISCUSSION

Bearing of the Rodents on the Age of the Deseadan

The Deseado is sufficiently older than the Colhué-Huapí so that all genera of rodents, and practically all genera of other mammalian groups, are different in the two horizons. If the criteria on which these South American rodent genera are based are comparable to the criteria distinguishing their contemporaneous North American relatives, the gap between the Deseado and Colhué-Huapí is much greater, for example, than that between the early Oligocene Chadronian at Pipestone Springs, Montana, and the middle Oligocene Brulé of the "Oreodon Beds" of South Dakota. Of the seven rodent genera from Pipestone, *Prosciurus, Ischyromys* and *Paradjidaumo* are represented in the Brulé; *Titanotheriomys* probably is; and *Adjidaumo* is found in contemporaneous deposits not in South Dakota. This leaves *Pseudocylindrodon* and *Cylindrodon* as the only rodent genera present at Pipestone but not in the "Oreodon Beds," and the former is represented only by a single specimen. This comparison suggests that the gap between the Deseado and the Colhué-Huapí may represent most of the Oligocene.

Since, however, no rodents are known from South America earlier than the Deseadan, we are convinced (as pointed out below) that they reached that continent during the long post-Mustersan hiatus. Once members of this order reached the relatively virgin field of South America, they certainly underwent a very rapid initial radiation, and this would have lasted until the rodents had occupied most of the available niches. Therefore, such an evolutionary development would have involved less time than a similar amount of evolution in North America, where the niches were already filled.

Intercontinental correlations would be greatly aided if we knew the detailed derivation of the Caviomorpha. Of the known possible ancestors, however, we believe *Rapamys* to be the most probable candidate (see below). This rodent, known from the late Eocene Duchesnean of North America, could be distantly ancestral to all the Deseadan rodents. If so, the morphologic change was certainly much greater than that between the Deseadan and Colhuehuapian rodents, being on the subordinal or familial rather than the generic level. Of course, if the argument for rapid post-Deseadan evolution, outlined above, is valid, that for rapid pre-Deseadan evolution would be even more so.

A combination of these lines of reasoning would suggest that the Deseadan is early Oligocene, but probably not earliest Oligocene, being perhaps contemporaneous with typical Chadron in North America; the Colhuehuapian is perhaps early Whitneyan.

If the Deseadan caviomorphs were not derived from *Rapamys* or a close relative, all other known possible ancestral forms would be middle Eocene or earlier. Such an ancestry would allow the age of the Deseadan to be shifted back toward the beginning of the Oligocene, but probably not as far as into the late Eocene. Therefore, no matter what the ultimate source of the Caviomorpha, it would seem probable that we are here dealing with an early Oligocene fauna. Schaub (*in* Stehlin and Schaub, 1951, p. 41) has expressed a comparable opinion.

The Relationships of the Deseadan Rodents to Later Forms and to Each Other

The problem of the relationships of these rodents is a twofold one. On the one hand, is the question of their affinities to each other and to those that follow them in time; on the other, is the broader question of the origin of the indigenous Neotropical rodent fauna as a whole.

The second part of the first question — the relationships of Deseadan to later forms — has been gone into in the discussions on the preceding pages. We believe that it has been satisfactorily demonstrated that *Platypittamys* is very near the direct line of the Octodontidae and is structurally very close to the ancestry of all the rest of the fauna except *Protosteiromys;* that the two species of *Deseadomys* are essentially ancestral to the *Adelphomys* group of the Echimyidae; that *Cephalomys* and *Litodontomys* may be referable to the Dasyproctidae, although their precise relationships to later members of the family cannot be decided at present; that *Scotamys* is a broadly ancestral member of the Chinchillidae; that *Asteromys* and *Chubutomys* are ancestral members of the two subfamilies of the Eocardiidae; and that *Protosteiromys* is on or very near the direct line of the Erethizontidae.

It would appear at first glance, therefore, that the Deseadan rodent fauna was highly diverse, almost as much so as later ones. Representatives of seven families and of all four of the recognized superfamilies are present. In point of fact, however, this heterogeneity is to an extent an artifact of taxonomy that tends to mask the essential homogeneity of these forms. These animals are widely separated in the scheme merely because a vertical classification best expresses the fact that the Deseadan forms can be traced forward into groups that subsequently become highly distinct from each other. That the ancestors of the various later groups were still close to each other structurally as well as genealogically is rather vividly demonstrated by the differences of opinion concerning the relationships of *Cephalomys,* which of course resulted from this similarity.

Wood (1949) has pointed out that the molars of all indigenous South American rodents suggest derivation from forms with four transverse crests above and below — the pattern shown by the early Octodontidae and Echimyidae. Winge (1887) had much earlier advanced a similar opinion, and it would also appear that Ameghino, with his customary insight, had implicitly recognized this—witness the repeated use of *Acaremys* as a basis for comparison in his descriptions of the early forms. Scott (1905, pp. 387-388) also entertained an essentially similar opinion, but without mentioning *Acaremys* specifically. We believe that the present study goes far towards establishing the validity of this view. Except for *Protosteiromys* and *Cephalomys*, every Deseadan rodent, of which the original upper molar crown pattern can be made out, conforms fully with the four-crested pattern. The lower molars of all are or may be presumed to be four-crested, save only *Deseadomys loomisi.*

There is no suggestion in any of these forms that the crests were surmounted by numerous small cuspules. Where an evolutionary sequence can be traced, rodents that have such a pattern can be shown to have been related (just as in the Proboscidea) to earlier forms whose crests were made up by ridges connecting the basic tribosphenic cusps. This is true for the cuspidate Recent *Dasyprocta*, *Myoprocta* and *Cuniculus* (Landry, 1957a, p. 47) which contrast with the crested Miocene *Neorcomys* among the Caviomorpha, for the Geomyoidea and for some murids. Such cuspules are present in the Hystricidae, but the phylogeny of this family is essentially unknown. We therefore disagree completely with Landry's statement (*op. cit.*, p. 48) that the "low-crowned teeth of erethizontids and echimyids are specialized and derived from [the] early cuspy tooth type" found in "low-crowned, primitive hystricids, which I believe to be close to the original tooth type in the Hystricomorpha." (Incidentally, his reference at this point to pl. 1, d, which does not exist, probably refers to pl. 2, a, which is a hystricid.) Landry's whole concept of dental evolution appears to us to be completely erroneous and based on a series of misconceptions and misinterpretations. He observes the presence of teeth with a multiplicity of cusps in a variety of late Tertiary and Recent caviomorphs and hystricomorphs and states that the pattern of cross crests and folds does not appear until after some wear. He believes that "this breaking up of the crown into a number of cuspules may have been a fundamental adaptation to the propalinal grinding of hystricomorph teeth" (*op. cit.*, p. 88), and he concludes that "such an arrangement suggests at once that the cusps are primitive and the infolded pattern derived" (*op. cit.*, p. 85). As he recognized, this observation is not original; it has led various observers to draw the now thoroughly discredited ultimate conclusion, namely that rodent teeth (or placental teeth) were derived from teeth of multituberculates, a conclusion in which Landry does not concur (*op. cit.*, p. 89). In fact, he states (*op. cit.*, p. 90) that he believes "that this multiplication in cusps is connected with the adaptation to propalinal grinding." It may or may not be true that a multiplicity of cusps is correlated with an adaptation to propalinal grinding, but it certainly cannot be assumed that such a multiplicity was inherited from a common ancestral "hystricomorph" stock. Furthermore, Landry has provided no evidence in support of his conclusion regarding the primitive nature of a multiplicity of cusps, except to state that "If a structure occurs in a group in many different lines, we assume that it was derived from the basal members of that group unless there is other evidence that it arose through parallelism in the different lines. Almost exactly the same pattern of change with wear as that of hystricids is found in the New World genera *Cuniculus* and *Dasyprocta* . . .'' (*op. cit.*, p. 85). A little later, however, he states that ''The same general folded type of tooth appears in many lines of rodents not particularly related to each other: beavers, theridomyids, eomyids, rhizomyids, cylindrodonts, as well as porcupines, and unless we assume, as do Stehlin and Schaub (1951) and Schaub (1953), that all these diverse rodents came from a common source, we must believe that the infolded crown arose through convergence in the different lines'' (*op. cit.*, p. 87). Nowhere does Landry offer any explanation as to why the presence of cuspules in several forms is a more significant indication of relationship than is the presence of a folded crown, and the only conclusion we can reach, from a careful study of his paper, is that his opinion that the multicusped crowns are primitive derives from his conviction that all hystricomorphous rodents are specially related and that the Hystricidae are among the more primitive members of the group. Whether or not these last two statements are correct (and we doubt both of them), all evidence of mammalian dental evolution is opposed to the primitiveness of multicuspidation. When he states that ''the intermediate stage between such a tritubercular tooth [as that of late Paleocene species of *Paramys*] and the teeth of hystricomorphs should show a multiplication of cusps tending toward the condition seen in the unworn teeth of *Atherurus*'' (*op. cit.*, p. 90), he is indicating a lack of familiarity with the known facts of mammalian dental evolution.

The exceptions to the general rule that all Deseadan rodent molars are four crested require discussion. We believe that in *Protosteiromys* the forward shift of the metaloph and the derivation of as large a neoloph as is present might require a considerable lapse of time. The Erethizontidae may have been the first group to diverge from the ancestral stock, the split perhaps going back to the late Eocene. The differences in the skull and skeleton between the Santa Cruz erethizontids and remaining contemporary caviomorphs support this point of view, as does the fact that the Recent Erethizontidae are myologically rather distinct from the remaining caviomorphs. Moody and Doninger (1956, pp. 52-53) report that the Erethizontidae appear to be as distinct serologically from the other caviomorphs they tested (*Cavia* and *Dasyprocta*) as either is from the Hystricomorpha (*sensu stricto*), and they suggest the possibility that the erethizontids had been independent since they split off from the Paramyidae, and that, therefore, a separate suborder is needed for this family. Vanzolini and Guimarães (1955a, p. 30; 1955b, p. 346) point out that the Erethizontidae are parasitized by an isolated stock of trichodectid Mallophaga, suggesting that they are very distantly related to other caviomorphs. Although there can be little question that the erethizontids were separated from the other members of the Caviomorpha at an early date, we feel that serologic and parasitologic evidence is difficult to evaluate, and that, at least for the time being, it is advisable to consider that the erethizontids are merely an early offshoot of the central caviomorph stock.[31]

The structure of the upper molars of *Cephalomys* has been discussed above (p. 333). Derivation from the four-crested pattern seems certain and the loss of the metaloph and the shift of the neoloph anterointernally probably required no longer a time than origin of the neoloph in the erethizontids.

The presence of only three crests in the lower molars of some early echimyids and the incomplete development of the fourth crest (metalophid) in others is at first glance perplexing. However, this is certainly a case of secondary suppression of the metalophid. The structural sequence *Platypittamys—Deseadomys arambourgi — D. loomisi* shows how such reduction took place. The metalophid is an unstable crest in a variety of later caviomorphs.

The premolars of the Deseadan genera are basically similar, uppers to uppers, lowers to lowers, and are notably less complicated (and therefore, we believe more primitive) than the molars (this would certainly be the case also in those forms, *Protosteiromys, Chubutomys*, and *Deseadomys loomisi*, whose premolars are not yet known), something that is by no means true of all later forms. P^4 is throughout much shorter than the molars and three-crested, the metaloph being absent or minute. Two types of P^4

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[31] Fields (1957, p. 351) has very tentatively suggested the possibility of a relationship between the Erethizontidae and the Dinomyidae, pointing out certain resemblances between the two in the auditory region and in the fusion of cervical vertebrae. We are not certain as to the significance of the auditory region (Fields' figures show differences as well as resemblances), and such characters as molar structure and the absence of any trace of a lateral process in dinomyids argue against close relationship. Ray (1958, p. 8), in a study of cervical fusion in dinomyids and erethizontids, questions this feature as an indication of close relationships between the two families.

occur. In the first, represented by *Deseadomys* (and probably *Protosteiromys*) the protoloph and metaloph were joined by a mure, as in the molars, as well as being joined lingually through what seems to be a hypocone. In the second, represented by *Scotamys* and *Cephalomys,* there is no mure and the combined anteroloph and protocone sweep around the inner face of the tooth to join the posteroloph posterointernally. *Platypittamys* combines the features of both and shows how each could have arisen from a common ancestral form. The difference is not fundamental, in fact the anteroloph becomes separated in later dasyproctids. It seems likely that a division into comparable structural types occurred in lower premolars, but the details are not clear.

Landry (1957a, p. 87-88) argues that a study of the pattern of the deciduous teeth can give us valuable clues to the "conditions which were present in the ancestral teeth . . ., since the milk dentition, being more or less transient, might not be so much affected by the selection pressures which were operating to change the permanent dentition. However, we cannot accept all the conditions found in the milk teeth as primitive, because there is always the possibility that the milk dentition has been subject to selective pressures of its own and has evolved special characters in response to them. . . ." We are in complete agreement with this last statement, and feel that a study of the milk teeth, while very important in understanding the evolution of the milk teeth, has little or no bearing on the ancestral condition in the permanent teeth. We therefore must conclude that the presence of cuspules on "the unworn milk premolar of *Coendu* . . . strongly reminiscent of an unworn cheek tooth of *Dasyprocta* or *Atherurus*" is merely an interesting observation and cannot be considered evidence "that the surface of the primitive hystricomorph cheek tooth was made up of a series of small cuspules. . . ." (*op. cit.*, p. 88).

Having briefly recapitulated the evidence demonstrating the essential morphologic unity of the dentitions of the Deseadan rodents, it is now necessary to do the same for the degrees of their divergence. It is at once obvious that a very distinctive group is that formed by *Scotamys*, *Cephalomys*, and *Litodontomys,* representatives of the Chinchillidae and Dasyproctidae.

The first two genera share nearly every dental feature, have a distinctive P^4 and are either hypsodont or hypselodont. They thus stand sharply apart from the rest, which is of course the warrant for brigading them in the same superfamily, a step taken in a preceding section. *Chubutomys,* representing the Eocardiinae, is close morphologically to the lower-crowned luantine, *Asteromys.* The other brachyodont to mesodont genera fall into two groups. The erethizontids, even this early, stand well apart (Wood, 1949, p. 5), certainly as much as do the contemporary chinchilloids; they are essentially modern as regards their molars. The cavioids do not have a P^4 of the chinchilloid type, and *Asteromys* and *Chubutomys* reveal that the basic four-crested pattern was present in the lower molars, at least, of the early representatives. We are strongly inclined to believe that the cavioids arose from the octodontid stock subsequent to the divergence of the chinchilloids, and that both of these separated somewhat later than did the erethizontoids. Our conception of the relationships and phylogeny is graphically shown in Figure 34.

Differentiation of the echimyids, the octodontids and the eocardiid *Asteromys* would appear to be relatively slight and could have been accomplished in a very small fraction of a geologic epoch. The time required for the evolution of the hypselodont to sub-hypsodont Deseadan chinchilloids and of the hypsodont eocardiid *Chubutomys* is another matter. Ordinarily, it would be assumed that hypselodonty and hypsodonty such as that exhibited by *Scotamys* and *Chubutomys*, respectively, must have required considerable time for its evolution. Such an assumption would not be a safe one in the present instance, however. When the rodents reached South America, they found a vast area over which to spread and an almost virgin adaptive zone with niche after niche open to exploitation. The situation was ideally suited to radiation, and the population structures were in all probability such as to permit the most rapid evolutionary rates. Under such conditions, the acquisition of hypsodonty presumably does not take long, and it is entirely possible that the initiation of the caviomorph diversification may have taken place as recently as late Eocene time. That the rodents were still a rapidly evolving group in the Deseadan is revealed

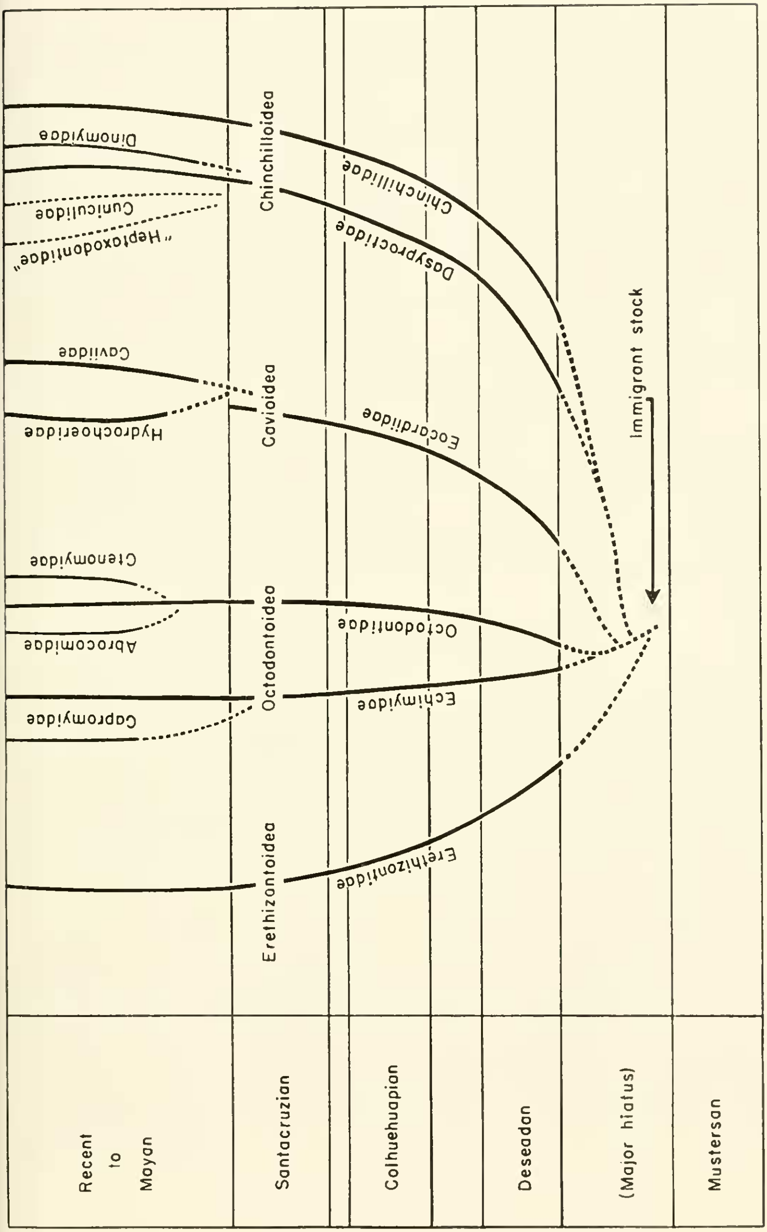

Fig. 34. Diagram illustrating the geologic ranges of the families of caviomorph rodents and our concept of their relationships.

by the considerable degree of advance that took place in all lines between Deseadan and Colhuehuapian time. The parallel case of late Pliocene and Pleistocene evolution of hypsodonty in the microtines can be cited in this connection. This point of view is a considerable contrast to that of Landry, who considers that the absence of any paramyids, as well as theridomyids and hystricids, in South America "suggests the possibility that no known rodent is ancestral to the hystricomorphs and that their intercontinental dispersal may have taken place considerably before the time usually postulated, perhaps as far back as the Early Paleocene" (1957a, pp. 81-82). This is, naturally, a possibility, but the hypothesis involves the assumption that pre-Deseadan rates of evolution in caviomorphs were extremely slow, and for this we see no evidence. Furthermore, as pointed out in more detail below, it also requires us to believe that in the Paleocene a relatively advanced group of rodents was in existence in the Northern Hemisphere, and that this group then disappeared from that hemisphere to be replaced (or displaced) in the early Eocene by the less advanced paramyids. This we regard as unlikely in the extreme.

The Origin of the Deseadan Rodents

The relative uniformity of the Deseadan caviomorphs leaves little doubt that the entire South American stock represents a development from a single invasion. A number of problems still remain to be considered, however. These are: (1) from what region did the ancestors of the caviomorphs come; (2) at what time did the invasion occur; and (3) what group of rodents was ancestral to the caviomorphs. These questions will be discussed in order.

The similarities between South American and African rodents tempted many authors to derive the former from the latter by a direct transatlantic invasion via a land bridge. Current opinion seems practically unanimous that there could not have been direct connection between Africa and South America, either by bridge or by former continental juxtaposition, at any time when rodents could have utilized it, and that therefore the immediate source of the South American rodents must have been North

America (see for example Lavocat, 1951a, 1951b, p. 72; Schaub, 1953a, p. 391; Simpson, 1950, p. 375; Wood, 1950).[32] Landry (1957a, p. 91) suggests that the ancestral caviomorphs may have reached South America by way of the Greater Antilles, and thus ultimately be of North American derivation. On present evidence, this route is nearly (though not quite) as logical a postulate as the alternative route through the then Central American archipelago. Landry's second hypothesis, that "hystricomorph" rodents reached the Antilles in the Paleocene is not a necessary part of his migration route hypothesis, and is discussed in more detail below. Viret (1955, pp. 1563-1564) is more cautious on the whole problem, and concludes: "Le problème du peuplement de l'Amérique du Sud par les Rongeurs reste une énigme qui ne peut être résolue dans l'état actuel de nos connaissances."

Simpson (1950, p. 375) and Wood (1950) have discussed the question of arrival of rodents over a land bridge or by rafting. Both reached the conclusion that the rodents must have entered South America by the latter method, because both interpreted the evidence as showing that the invasion took place in the latter part of the Eocene, a time at which no other mammals entered South America from North America, with the possible exception of the primates. We fully agree with this conclusion. Recently, however, Schaub has suggested that the source of the Caviomorpha is to be found in rodents with a *Theridomys*-like tooth pattern that reached South America in the Eocene, Paleocene, or even earlier (1953a, p. 393). Lavocat (1956, p. 55) goes part way with Schaub, suggesting that the similarities between the Caviomorpha and the Hystricomorpha (or Nototrogomorpha and Palaeotrogomorpha) could be explained on the assumption that the two groups were remnants of a homogeneous Paleocene

[32] That the ancestral South American rodents might have been transported by natural rafts directly from Africa to South America, or, contrariwise, the ancestral hystricomorphs (*sensu stricto*) from South America to Africa, in the latter part of the Eocene are views seldom advanced. We do not take either possibility very seriously, particularly not the former. Hystricomorphs (*sensu stricto*) do not appear to be raft-prone: they have failed to reach such islands as Madagascar and the Philippines proper, not to mention New Guinea and the continent of Australia. We wish to point out, however, that, in the light of current knowledge of the paleontology and zoogeography of the Rodentia, raftings of this sort are the only alternatives left to those who insist on direct caviomorph-hystricomorph relationships. Otherwise, as we indicate below, there seems to be no escape from the conclusion that the ancestors of the South American rodents lived in North America during the latter part of the Eocene, and that, in this continent at that time, they could only have been protrogomorphs and, in all probability, paramyids.

rodent population of the Northern Hemisphere that had penetrated South America and Africa. On the other hand, he had previously concluded (1951a, p. 38) that any resemblances between New and Old World forms must be pure parellelism. Landry (1957a, pp. 90-91) strongly supports the caviomorph-hystricomorph distribution as indicative of a Paleocene radiation. In view of the weight of this continued support for close relationships between South American and Old World forms, the problem of the time of origin of the caviomorphs must be reconsidered.

There was certainly an early immigration from North America to South America, in late Cretaceous and/or early Paleocene time, which provided the ancestors of most of the indigenous South American Tertiary mammalian fauna (Simpson, 1950, pp. 368-373). These immigrants may well have reached the continent by rafting (Darlington, 1957, p. 364; Patterson 1958b, pp. 11-13). This, apparently, would be the source envisioned by Schaub and Landry, although, as already mentioned, Landry (1957a, p. 91) hedges a bit by suggesting that perhaps the "hystricomorphs" reached the Greater Antilles in the Paleocene, but did not reach South America until early Oligocene. Lavocat specifically suggests (1956, p. 55) that, after making such a Paleocene invasion, the rodents could well have lived in parts of South America whose Tertiary history is still unknown. Although this is undoubtedly a hypothetical possibility, it does not seem at all probable to us, for several reasons. There are actually three problems to be discussed here: whether there could have been any rodent invasion much before the end of the Eocene; whether there could have been an invasion by any Paleocene rodents (Lavocat, 1956, p. 55); or whether there could have been an invasion by Paleocene theridomyids. Establishment of the improbability of any one of these would establish the improbability of any of the others.

Since the Deseadan rodents are, as pointed out above, a closely related stock, and since they were at this time near the beginning of a rapid differentiation which continued through Colhuehuapian into Santacruzian time, it seems to us almost certain that there was a single common ancestor of the Deseadan rodents which existed not too long before Deseadan time. All previous history of South American rodents must have involved a relatively small amount of evolutionary progress, with little or no adaptive radiation.

No trace of a rodent has been found in the Paleocene Río Chico of Patagonia, in the Paleocene Itaborai fauna of southern Brazil, or in the Eocene Casamayoran and Mustersan of Patagonia. It could be supposed that these animals might have been living in northern South America during the earlier part of the Tertiary, but we regard this as extremely unlikely. The Pleistocene faunal history of South America and the Recent faunal history of Australia reveal what happens when forms fitted for life in a given adaptive zone are suddenly confronted by invaders higher in the scale of evolutionary progress that happen to be fitted for the same zone; the forms lower in the scale do not linger long and the invaders spread with the greatest rapidity. Had any rodents reached South America before late Eocene time, we believe it to be essentially axiomatic that their descendants would have swept all before them within their adaptive zone, which was then only marginally occupied (by polydolopids, groeberids, typotheres and hegetotheres), and would surely have put in an appearance in Patagonia. Moreover, we see only one probable explanation, other than their recent arrival in South America, for the sudden burst of the rodents just before Deseadan time. This would be the rapid development of new structures that enabled them to compete much more successfully with their non-rodent rivals. The only such structures of which we are aware would be the multilophate cheek teeth and the enlargement of the masseter muscle and its expansion through the infraorbital foramen. While we believe that such changes did take place in the latter part of the Eocene, their development at this time in the ancestors of the caviomorphs, had these been in the continent at a much earlier date, would establish that these ancestors were non-hystricomorphous in teeth and masseter; would eliminate the possibility that any Old World hystricomorph-like rodent had any special relationship with them; and, we believe, would lead by a process of elimination to our interpretation of the late Eocene caviomorph ancestor as being a paramyid or sciuravid. It appears to us, however, virtually certain that rodents did not reach South America until after the close of the Mustersan, which, according to the best recent estimate (Simpson, 1940), is approximately of mid-Eocene age. They therefore arrived sometime during a great hiatus in South American faunal history — the gap in our knowledge that extends from Mustersan to Deseadan, from approximately mid-Eocene to early Oligocene. The precise time of their arrival within this interval cannot now be determined.

Rejection of the possibility of a Paleocene rodent invasion of South America requires consideration of the time of origin and of early geographic radiation of the rodents. This is something about which virtually nothing is known, except that rodents do not become numerous until the early Eocene and that only a single earlier species, *Paramys atavus,* is known from the late Paleocene (Jepsen, 1937). How much earlier the rodents were in existence we do not know. Wilson (1951) has argued that the order, as such, probably arose about late Paleocene time, agreeing with Jepsen (1949) that the abrupt replacement of multituberculates by rodents at the beginning of the Eocene argues against the latter having been in existence for more than a short time previously. We believe that if rodents had entered South America in the Paleocene they would surely have been widespread in North America at that time and hence would be represented in our collections from that continent, as well as from the Eocene of South America. This, of course, is arguing from negative evidence, and anyone who wishes to hold contrary views is free to do so. However, it is surely unwarranted to conclude that such a hypothetical group of rodents were so much more highly specialized than any of the known early Eocene rodents that they must have been hystricomorphous, and to assume, further, that they acquired a world-wide (or nearly world-wide) distribution is piling hypothesis upon hypothesis, and is logically indefensible. We do not wish to argue the question as to the date of the separation of the rodents from the insectivores, or as to the rates of pre-Eocene rodent evolution, because we know of no new evidence bearing on these subjects.

The possibility of a theridomyid having reached South America in the Paleocene, as envisioned by Schaub (1953a, p. 393), has additional arguments against it. As Viret has observed (1955, p. 1564, footnote 1), the *Theridomys*-pattern was not present, even in Europe, in the Paleocene. As pointed out above, we believe that we can trace the development of five-crested caviomorphs from four-crested ones, and not vice versa. If we are correct in this interpretation, the theridomyids again could not have been ancestral to the Caviomorpha, and we should have to rely for ancestors on four-crested or incipiently four-crested North American forms, of which a number are known. Our arguments on this point are involved in the whole question of the basic pattern of rodent teeth and the primitive stock of the rodents, which are discussed below. But we feel very strongly that, whatever the Paleocene rodents were like, they had not yet attained the complexity of structure that would permit them to be called theridomyids, or indeed to be referred to any currently recognized groups except the Paramyidae.

We therefore feel that the most probable explanation of the known history of South American rodents is that they arrived, by island-hopping, from North America, sometime in the latter part of the Eocene.

Ancestry of the Caviomorpha

Having attempted to answer the questions as to the geographic source of the Caviomorpha and the time of their arrival in South America, we come to the question of the group of rodents that gave rise to them.

Stehlin and Schaub (1951) have presented a major and exceedingly valuable study of the development of the cheek teeth in rodents, which we will discuss more fully below. But, on the basis of this study, Schaub has strongly supported the Theridomyidae as being the ancestral stock of all multi-crested rodents. We have tried to show above that the ancestral caviomorphs were not pentalophate, as is *Theridomys*, but tetralophate, and that the development of a fifth crest, when it occurs, is a strictly local phenomenon in South America. It would be advisable, however, to review in this connection the possible origins of each of the known Deseadan rodents.

As indicated above, *Platypittamys* must be very close to the basic type from which all the rest of the caviomorphs were derived. It clearly could not be descended from the Theridomyidae, but shows numerous structural similarities to such North American rodents as an undescribed lowest Eocene paramyid and the Duchesnean *Rapamys*, as far as the latter is known. The pattern of the teeth (particularly of P^4) of *Deseadomys* is very different from that of the Theridomyidae. Without exerting what we consider to be an excessive strain on the imagination, the only known source from which it could ultimately have been derived would be a paramyid or sciuravid. *Deseadomys* shows no close relationships to any Old World forms, and particularly not to the theridomyids or to *Phiomys*. It would be possible to imagine its descent from such forms, by the loss or fusion of crests, but there is no evidence for this and it seems clear to us that derivation was from the octodontids as represented by *Platypittamys*. It is therefore much simpler and more reasonable to assume the ultimate derivation of *Deseadomys* from North American paramyid ancestors.

Landry (1957a, p. 94) states, "Wood's proof that South American hystricomorphs could not be related to Old World hystricomorphs consists entirely of reasons why the teeth of *Platypittamys* could not be derived from those of the theridomyids." There really *was* a little more to the story, but leaving this aspect of the matter aside we must point out that, in 1949, derivation of Hystricomorpha (*sensu lato*) from the theridomyids was a hypothesis very much to the fore and Wood had no choice but to discuss it. The idea is still current — in greatly expanded form (cf. Stehlin and Schaub, 1951) — and we still think it necessary to discuss it. As we have shown above, the third crest in caviomorph upper molars is a metaloph, and, as may be seen from Stehlin and Schaub's figures (16, 21, 26, 29) showing portions of the sequence (which we believe to be phylogenetic or nearly so) running from *Paramys* to *Decticadapis* to *Adelomys* to *Theridomys*, the third crest in theridomyids is a mesoloph. The considerable superficial resemblance notwithstanding, the two molar types are quite different, despite Landry's remark (*op. cit.*, p. 95) that "A comparison . . . shows that exactly the same elements are present in both. . . . The only difference is in the assignment of names to them." As regards the Hystricomorpha (*sensu stricto*), we suspect the third crest of the upper molars to be a mesoloph. Hystricomorph history is very poorly known, however, and since this homology has not yet been proven phylogenetically, the possibility still exists that the third and fourth crests of hystricomorph molars and of such caviomorph molars as possess five crests may be comparable. Even if this should prove to be the case, it would not affect the evidence indicating that the fifth crest of caviomorphs came into existence after arrival of the group in South America, and thus quite independent of its origin in the Hystricomorpha. We may state our full agreement with Landry — and with Lavocat before him — as concerns his observation that the sciurognath type of jaw characteristic of the Theridomyidae tends to bar the family from the hystricomorph — and caviomorph — ancestry.

Cephalomys could likewise have been ultimately derived from a North American Eocene paramyid, perhaps something like *Rapamys*, through intermediate stages similar to *Platypittamys*. In view of the pattern of P^4, it would seem almost certain that it was not descended from forms with quadrilophate upper premolars. This would eliminate most forms that have been suggested as being the ancestral stock, and particularly the theridomyids (Fig. 35A), which have a completely molariform upper premolar. The theridomyids also show no particular similarity in the structure of P$_4$. The presence of a mesoloph in the theridomyid upper teeth is a notable difference from the pattern of *Cephalomys*. The patterns of the lower molars are similar in a very general way in the two groups, but by no means sufficiently so to indicate special relationships. The pattern of dm$_4$ appears rather similar at first glance, but it is not identical. The posterolophid and hypolophid of the two seem closely comparable. The mesolophid in *Theridomys* (Fig. 35B) lies well behind the anterior part of the tooth, and the metalophid is connected with both ends of the anterolophid whereas in *Cephalomys* (Figs.

Fig. 35. Cheek teeth of *Theridomys* x 5. *Theridomys rotundidens* Schlosser, LP^4-M^3, Munich no. 1879–xv–182 a-d; *B*, *Theridomys speciosus* Schlosser, Rdm$_4$-M$_1$, Munich no. 1879–xv–183 a-b.

20A, B) there appears to be no mesolophid, and the three anterior cusps, presumably derived from the anterolophid, connect with the middle of the metalophid. Although these are rather notable differences, how much weight should be attached to them is uncertain, due to our general lack of knowledge of the evolution of rodent deciduous molars. *Scotamys*, which, as has already been shown, is fundamentally similar to *Cephalomys*, is also derivable from the octodontids. The same applies to the two cavioids, *Asteromys* and *Chubutomys*.

Protosteiromys, as already noted, is the only Deseadan form that shows any appreciable similarity to the theridomyids, and much of the resemblance is due to the presence of a neoloph, giving an incipient five-crested pattern. Even if the similarities in tooth pattern had originated in the same way, which, with Friant (1936b), we do not believe, it would still be simpler to postulate an origin of *Protosteiromys* from the Octodontidae, rather than to assume that one Deseadan rodent originated from an Old World group while the others had a different ancestry. Since the last crests to develop, the neoloph (fourth crest) in *Protosteiromys* and the mesoloph (third crest) in the theridomyids, are not homologous, we believe the octodontid relationship to be the only possible one. These arguments, of course, would have no weight with anyone who adopts Landry's point of view that "the pattern of the occlusal surface of almost any tooth *could* be derived from any other" (1957a, p. 89), but this does not appear to us to detract from the validity of our argument. Since the Old World theridomyids must, it would seem, be ruled out of the caviomorph ancestry, the only possible source of this ancestry is some North American rodent, unless, with Landry, one prefers hypothetical ancestors with hypothetical molar structure, or fancies transatlantic rafting. Such an ancestral form would have reached South America from North America by island-hopping. Since all the South American forms could hardly have been derived from anything else, and since it seems virtually certain that the Deseadan forms were derived from a single source, this appears to be the only logical interpretation of the available data. The similarities between the Hystricomorpha and the Caviomorpha must then be parallelisms. We feel very strongly that parallelism is a dominant character of rodent evolution, and particularly of rodent dental evolution (Wood, 1937b, 1947, 1950), and that very similar structures may appear over and over again within the order. Lavocat (1956) argues this same point of view. For all these reasons, we do not feel that any known theridomyid, or any ancestral rodent which was sufficiently advanced so it would be called a theridomyid, could be ancestral to the Caviomorpha, and the possibility of such relations between theridomyids and hystricomorphs (*sensu stricto*) also seems to be ruled out.

The resemblances of the thryonomyids and petromurids to certain caviomorphs have been cited as indicative of relationships. As pointed out by Wood (1950), if there were a close relationship, which is most unlikely, it would indicate that the African forms more probably had a South American ancestry, rather than vice versa. Landry (1957b) has recently demonstrated that the petromurids do not resemble the octodontids to any significant extent.

There are only two known groups of North American rodents that could be ancestral to the Caviomorpha, on the basis of their tooth structure.[33] These are the Sciuravidae and the Paramyidae. The Sciuravidae show a basic four-crested pattern that could have been ancestral to that of the Caviomorpha. There are a number of variant types within the sciuravids, which have not been thoroughly studied. But none of the known material shows any suggestion of an enlargement of the infraorbital foramen, and none that we have seen suggests the inflected angle of the hystricognath type found in caviomorphs. For the present, at least, we regard the sciuravids as a possible source for caviomorphs, but not a probable one.

The review of the Paramyidae, in progress by Wood, has revealed that a four-crested pattern develops within this family from a basic tribosphenic ancestral type. Structures of this sort

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[33] Landry (1957a, pp. 88-89) objects to the use of dental anatomy in studying rodent evolution, pointing out that different students have interpreted tooth structures and tooth relationships differently, which is, of course, equally true for characteristics of the other parts of the animals. He objects to "the notion that by demonstrating that a certain tooth *could* be derived from another, we demonstrate that it *was* so derived. . . . Proof that one tooth pattern was derived from another requires corroborative evidence from the study of other structures, or a series of intermediate stages. Particularly is this true in the study of rodents, where the same tooth pattern has evolved again and again in different lines" (*op. cit.*, p. 89). Having made this statement, he then proceeds to ignore it over and over again in his discussion of hypothetical evolutionary trends in other structures where parallelism is just as complex as it is in tooth patterns.

have arisen several times within the family in different lines, in each of which the temporal sequence is sufficiently complete so that it is obvious that this is what was taking place. In one line, leading through *Reithroparamys* to the Duchesnean *Rapamys*, acquisition of this dental pattern is associated with an enlargement of the infraorbital foramen. Unfortunately, the known material of *Rapamys* is very fragmentary, and it is impossible to be sure of the exact size of the foramen. Nothing is known of the structure of the angle in the genus, although, as pointed out by Landry (1957a, p. 82), the angle of *Reithroparamys* suggests an incipient stage toward a hystricognath jaw. Therefore, all that can be stated with certainty is that *Rapamys* seems to be closer to the caviomorph type than does any other currently known North American rodent. An undescribed earliest Eocene paramyid in the Amherst College collections, represented by a partial skull, a jaw, and fragments of the skeleton, has some similarities to the Deseadan rodents, particularly in the pattern of P^4. The infraorbital foramen is that of a typical paramyid, but the angle appears to be arising lateral to the incisive alveolus, making this a hystricognath paramyid. It is possible that this form may bear some relationship to the caviomorph ancestry.

Geographically, then, we believe that the Caviomorpha were derived ultimately, and perhaps directly, from North American rodents, which, taxonomically, would be referred to the Paramyidae. The sequence is, of course, far from complete. The South American rodents were not descended from immigrants from Wyoming, but rather from rodents that lived in some part of Middle America or southeastern United States, regions from which the Eocene mammalian faunas are essentially unknown. When and if these are discovered, we feel that they will include paramyids, probably related to *Rapamys*, which will show a number of pre-caviomorph specializations. The discovery of sciuravids at Guanajuato, Mexico (Fries, Hibbard and Dunkle, 1955), suggests that there are deposits of the critical age in this area that may eventually produce additional rodents that will help to solve this important problem.

Problems of Rodent Phylogeny

The discussion above on the origin of the caviomorphs appears logical to us on the basis of our ideas as to rodent evolution. Not everyone is in agreement with these, and we must therefore explain why our opinions differ from those of some other students.

Stehlin and Schaub (1951) present a detailed analysis of rodent tooth patterns and their interrelationships. This work was unfinished by Stehlin at the time of his death in 1941, and was completed, with signed sections and unsigned insertions within brackets, by Schaub. Both authors have an unsurpassed background of study on fossil rodents, so that it is with some hesitation that we express our serious objection to a number of points they raise.

One of the main points of this major contribution, and the one of chief concern for the present study, is Stehlin's concept of a "*Theridomys-Trechomysplan*" in molar structure. This "plan" is believed by him to have been structurally derivable from the "trigonodonten Grundplan," represented by such forms as *Marmota*, and to have been structurally capable of giving rise to a wide variety of derivatives. The pattern found in the early Eocene rodents referred by us to the Paramyidae is not considered by him to represent the primitive rodent tooth pattern, in spite of its being the pattern of the earliest known members of the order, and in spite of the fact that it shows considerable similarity to the *Marmota* pattern. Nor is the paramyid structure considered to be intermediate between the "trigonodonten Grundplan" and the "*Theridomys-Trechomysplan,*" which leaves practically no known forms occupying such a position. Evidently considered as close structurally (Verwandten) to *Theridomys* are various African and European forms (*Phiomys, Sciuromys,* etc.) and *Eosteiromys* (including our *Protosteiromys*) and "*Parasteiromys.*" The morphological derivates of the "*Theridomys-Trechomysplan*" include a wide variety of groups: Hystricidae, Thryonomyidae and Bathyergidae, all the Caviomorpha of this paper (derivable morphologically, it would seem, via the Erethizontidae), Castoridae and Eutypomyidae, Rhizomyidae and Spalacidae — to give but a partial list.

It must be emphasized that, as Stehlin states (*op. cit.*, p. 351), this is a morphological study pursued essentially without reference to taxonomy and with but little reference to relative ages of the forms concerned. The work is in fact an undertaking carried out partially, but only partially, along the lines of what Davis (1949, p. 65) has dubbed the neoclassical school of comparative anatomy, although without reference in the bibliography to works of any of the chief exponents of this school, e.g., Naef, Kälin. It is no deprecation of the methodology characteristic of this approach to state that, in our opinion, its application, as partially carried out by Stehlin, to a single system of an order notorious for the parallelism that has occurred within it is not at this time very helpful. The ''*Theridomys-Trechomysplan*'' is a morphological abstraction that has, we believe, a limited phylogenetic — and also morphologic — application, and may well contribute to future misunderstanding. As Stehlin himself emphasizes, only an acquaintance with more than one structural system of a group through time can place our knowledge of taxonomy and phylogeny on a sound basis. For this very reason we are inclined to regard the inclusion of all forms that appear to show four or five transverse crests on their cheek teeth, whatever other variations may occur in the rest of their anatomy, among the structural derivatives of this ''plan'' as being a step away from a classification based on phylogeny and back toward a convenient pigeon-holing with no basis in the evolution of the rodents.

A rather large part of our objection to Stehlin's procedure is nomenclatural. To label this morphologic abstraction the ''*Theridomys-Trechomysplan*'' is, we believe, dangerous. To do so is to apply terms relevant in one frame of reference, the phylogenetic-taxonomic, to another that is admittedly non-taxonomic. Although it may not have been Stehlin's intention, no one can read this paper without feeling that there are at least implications that the arrangement in accordance with this ''plan'' is a phylogenetic one. This point of view has since been expressly adopted by Schaub (1953a, p. 394 *et seq.*), and the usage has spread to at least one standard reference work (Grassé and Dekeyser, 1955).

In neo-classical comparative anatomy, if it is to serve its purpose, interpretations (in this case anything that smacks of formal taxonomy) must be rigidly excluded from the methodological process and introduced only in the terminal interpretive phase. That the "*Theridomys-Trechomysplan*" was derived from the "trigonodonten Grundplan" is a reasonable assumption from the viewpoint either of neoclassical comparative anatomy or of interpretive phylogeny, but to assume that it is itself a single entity from either viewpoint is hardly warranted. Nor does it appear to us to be reasonable to assume that all the lower Eocene rodents are highly specialized and that none of the primitive ones appear until considerably later. Neither does it seem reasonable to assume that a family, whose known distribution is restricted to Europe, gave rise to a wide variety of forms living in all the rest of the world. At the very least, this is contrary to what has been observed in other orders of mammals. Without entering into a detailed neoclassical comparative anatomical analysis of rodent molars with "Aussen- und Innenantiklinalen und- synklinalen," it would seem to us that any such analysis should surely postulate, or at least entertain the possibility of, an ancestral stage ("plan") without a fifth crest; and that, in the interpretive phase of the work, the possibility that various forms with this crest may have passed independently through such a stage should be carefully considered.

If the "trigonodonten Grundplan," with anterior and posterior cingula, protoloph and metaloph, but no mesostyle or mesoloph (Stehlin and Schaub, 1951, Fig. 1) gave rise to the "*Theridomys-Trechomysplan*," it would seem almost (though perhaps not quite) necessary to assume that a four-crested pattern preceded the five-crested one. At the very least, a primitive four-crested stage should be considered as an alternative possibility to the postulate that the four-crested pattern is a specialization formed by reduction from a five-crested one.

This is one point where we feel that the "*Theridomys-Trechomysplan*" has been transferred from a morphologic to a phylogenetic concept by Stehlin and Schaub. For example, dealing with *Deseadomys* ("*Asteromys*"), they state: "Dass schon in der Deseadoformation Sudamerikas stark spezialisierte Formen vorliegen, beweist *Asteromys prospicuus*. . . . Die brachyodonten Zähne besitzen nur noch drei Aussensynklinalen; es fehlt anscheinend, wie bei *Acaremys*, die vierte'' (*op. cit.*, p. 60).

The transformation of one type of rodent tooth into another has clearly occurred independently on numerous occasions. For example, the change from brachyodont to mesodont or hypsodont teeth can be followed independently in the Geomyidae, Heteromyidae, Eomyidae, Theridomyidae, Sciuravidae, and Cricetidae, to name but a few cases, and the same was true, we believe, for the Caviomorpha. In each case, the original, low-crowned members of the group have rounded, plump cusps, or distinct traces of cusps, with a minimum of connecting crests. In each case, subsequent evolution accentuates the crests, giving rise to rather similarly appearing multi-crested forms. As far as we are able to interpret the evolutionary picture of the rodents, these animals represent a number of lines that evolved, independently, from ancestors that were primarily cuspate. On the basis of the time of occurrence of the earliest members of these groups, the ancestors must be sought not later than late Eocene for the geomyids, heteromyids, cricetids and caviomorphs; not later than middle Eocene for the eomyids and theridomyids; and not later than earliest Eocene for sciuravids. This, again, suggests to us that these various groups have developed independently of each other.

We believe that the early Eocene paramyids are the most primitive known rodents. The data supporting this point of view will be included in the review of the Paramyidae in preparation by Wood. Unfortunately, most published illustrations of the teeth of primitive paramyids are inadequate, but a few good ones are available (Stehlin and Schaub, 1951, Figs. 16, 17, 156, 157, 305, 306, 465 and 466). Within the Paramyidae, a series of lines can be traced, leading to greater specialization and gradual development of lophate teeth. Some of these lines we believe can be considered to lead to other, and more advanced, families (*Paramys* — *Decticadapis* — *Adelomys* — *Theridomys; Paramys* — *Sciuravus; Paramys* — later paramyids — sciurids; etc.), whereas others were doubtless sterile offshoots. But we believe that this early and middle Eocene radiation of the Paramyidae provided the source for the subsequent evolution of the rodents.

It is in the lack of allowance for the known parallelism that is found among the rodents, it seems to us, that Stehlin's analysis fails of being a completely neo-classical one, just as it is admittedly not a phylogenetic one. And it is here that the employment of the term "*Theridomys-Trechomysplan,*" rather than a descriptive, non-committal name, introduces an unnecessarily complicating nomenclatural factor. This term is associated with a well-known phylogenetic hypothesis (derivation of Hystricomorpha *sensu lato* from the Theridomyidae) that should never have been introduced into the morphological analysis. This phylogenetic hypothesis would be applicable at the very most only in part (Theridomyidae-Hystricomorpha *sensu stricto*), and even so limited an application as this now seems unlikely, since Lavocat has clearly indicated that this cannot be a true phylogenetic series for some of the Old World Hystricomorpha, and he has recently (1956, p. 54) suggested that the Theridomyidae are related to no known rodents except the Pseudosciuridae. We further believe that the analysis of the differences between the theridomyid and caviomorph cheek teeth given here destroys the validity of the "*Theridomys-Trechomysplan*" as a non-phylogenetic concept also, certainly so far as it applies to the caviomorphs.

The somewhat critical tone of part of the foregoing should not be interpreted as an expression of our opinion concerning Stehlin and Schaub's work as a whole. The volume is one of the most useful publications on rodents that has ever appeared, and will, we believe, rank with Tullberg as a classic that must always be consulted, particularly by anyone interested in rodent teeth. The clear and lucid descriptions, the magnificent figures and the stimulating taxonomic discussions by Schaub ensure for it a great and enduring value.

Part of our difference of opinion with Stehlin and Schaub over the primitive nature of the Paramyidae lies in the interpretation of the anterior end of the lower molars. This will be discussed at length by Wood in his forthcoming review of the Paramyidae, but we believe that the paraconid was lost before the first appearance of any rodents in the fossil record. There is, in the paramyids, a weak crest along the anterior face of the lower molars. This might be the last remnant of the paraconid-protoconid crest, or it might be a neomorph, but there certainly is no paraconid. When a cusp appears at the anterior end of lower molars later on in rodent history, we believe that it is clearly a neomorph, best called an anteroconid. This is the structure Schaub (1953b, pp. 8-9 and Figs. 11-12) calls a paraconid, and which he considers an important indication that Oligocene squirrels are the most primitive known rodents.

The recent discussion of "hystricomorph" relationships by Landry (1957a) falls into an entirely different category. This starts out as a comparative-anatomical study of rodents that have been classified as hystricomorphs at one time or another, and concludes, on the basis of a number of similarities of various kinds, that they are related. The resemblances exist, and in the absence of a fossil record would indeed justify retention of the Old and New World forms in one suborder. As matters stand, however, we are compelled to differ and to regard the resemblances as due to parallelism, not to special affinity in the sense of derivation from a common ancestral stock that was already "hystricomorph." Furthermore, we have to take exception to some of Landry's reasoning.

We cannot accept his view that structures appearing late in evolutionary history, such as the multicusped pattern of the molar teeth in some groups, are primitive. When a specialized character, which he considers as basic for the "Hystricomorpha," does not occur in some early members of the group, he considers that these members have secondarily reverted to the primitive rodent condition, a hypothesis requiring a degree of evolutionary reversal which appears improbable. For example, Landry considers the loss of the entepicondylar foramen to be a basic character for the "Hystricomorpha," stating that ". . . the fact that the entepicondylar foramen is almost never found in hystricomorphs indicates that it was lost early in the history of this group" (Landry, 1957a, p. 20). He adds that the only form he knows that had such a foramen was the Pliocene *Lagostomopsis*, in which L. Kraglievich found it in 14 out of 16 specimens. This he interprets as meaning that the lost entepicondylar foramen was reacquired by *Lagostomopsis*, and subsequently lost once more by its descendants. In this connection, however, he overlooked Wood's record (1949, p. 29) of the presence of this foramen in *Platypittamys,* which we consider as evidence that the foramen was present in the basic caviomorph stock, and independently lost in a number of lines. It should be emphasized that this form is the only pre-Santacruzian caviomorph for which we have any knowledge of the postcranial skeleton. As another example, Landry considers that fusion of the upper ends of the tibia and fibula ''may have been present in ancestral hystricomorphs'' (p. 19), overlooking the fact that there is no evidence of such fusion in *Platypittamys,* nor in the Santacruzian *Neoreomys* and *Steiromys* (Scott, 1905, pp. 397, 415). Having decided that a proximal fusion of the tibia and fibula may have been present in the ancestral ''hystricomorphs,'' and accepting that this may be a fossorial character, he suggests that the ancestral ''hystricomorphs'' may have been fossorial animals. He then states that the fossorial bathyergids possess some primitive rodent characters, such as a separate scaphoid and lunar, and that therefore they may be modified descendants of the ancestral ''Hystricomorpha'' (*op. cit.,* pp. 19-20). This we think is somewhat tenuous. His arguments in favor of the primitive nature of a multiplicity of cusps, of the value of the milk teeth in determining the primitive nature of the molar pattern, of a secondary decrease in hypsodonty in the teeth of the Bathyergidae, and his refusal to accept reasonably well documented evolutionary lines as being indicative of what really happened, seem to us to reflect a basic unfamiliarity with the fossil record and with the methods of study of fossils, without which no classification can hope to achieve a firm phylogenetic base.

Landry is unwilling to accept the results of detailed phylogenies of rodents based on tooth structure, stating ''. . . it is nevertheless true that where one observer sees similarities in teeth, another sees differences. The matter is so subjective that I believe that classifications of rodents based on similarities of the occlusal surface of the teeth are useless'' (*op. cit.*, p. 89), and he cites the fact that the same type of tooth pattern has evolved many times in the rodents. He is perfectly willing, however, to accept the evidence of structures where there is, and presumably always will be, no actual evidence of evolutionary sequence, such as the sacculus urethralis in the penis (*op. cit.,* pp. 16-17).[34] He believes that the presence of multiple cuspules in isolated instances among modern "hystricomorphs" is a clue to the ancestral pattern, but that the underlying structure of the teeth is not. He believes the structure of the angular process but not that of the infraorbital foramen to be fundamental; e.g., he places the Bathyergidae in the Hystricomorpha and eliminates the Pedetidae. He believes that the histologic structure of the incisor enamel is important, except presumably for such forms as *Pedetes* that do not fit his classification. He considers the fact that there are spines on the penis or a forward opening of the pterygoid fossa in "hystricomorphs" as indicative of relationship among these forms, but disregards these characters when they occur in non-hystricomorphous rodents (e.g. a forward opening of the pterygoid fossa in geomyoids), or passes over the absence of one of them in a group regarded as "hystricomorph" (e.g. lack of a forward opening of the pterygoid fossa in Ctenodactylidae). The evidence from auditory ossicles that he advances has been discussed above (p. 292). He believes that cranial foramina are worthless in rodent classification because there is considerable variability as to which nerves and blood vessels follow which paths, whereas this fact may well indicate that the cranial foramina and their contents are potentially very useful although at present poorly understood. In other words, in spite of his protestations to the contrary, we feel that Landry is setting up a key classification instead of a phylogenetic one. This is justifiable when the phylogenetic data are not available, and is justifiable as an adjunct to the use of data from phylogeny, but is not warranted when it is contrary to the data from the study of fossil rodents, as is the case with Landry's proposed classification. Finally, it seems to us, Landry is guilty, on a number of occasions, of assuming that a particular condition held true for the hypothetical ancestral "hystricomorphs,"

[34] We fully share Landry's interest in the remarkable distribution of the sacculus urethralis within the Rodentia, although we are unable to see quite eye-to-eye with him regarding the over-riding importance he attributes to it as a proof of the unity of Hystricomorpha (*sensu lato*). We note its occurrence in the Bathyergidae and the presence of a vestige (or rudiment?) of it in the Ctenodactylidae, groups which, with Lacovat, we would exclude from the Hystricomorpha (or Palaeotrogomorpha). Landry does not mention Pocock's finding (1922, pp. 412, 425) that the sacculus is lacking in *Lagostomus* — presumably a secondary loss, since it is present in *Chinchilla*. This absence so shocked Dathe, another student of this curious little structure, that he was almost prepared (1937, p. 54) to read *Lagostomus* out of the Hystricomorpha (*sensu lato*).

and then of using these assumed ancestors in an attempt to demonstrate the truth of some of his other hypotheses. Perhaps we do him an injustice here, but repeated reading of his work gives us this impression. A quotation from Landry succinctly illustrates our objections to his method of approach: "The usual procedure [in dealing with South American fossil rodents] seems to be to sort out the fossils into categories already set up on the basis of the morphology of the living forms, a procedure that is likely to be misleading" (*op. cit.*, p. 36). We agree heartily with this statement, which we feel describes precisely what he has done.

Classification of Rodents

This paper was first written toward the end of a period in which there had been growing dissatisfaction with the then prevalent division of rodents into Sciuromorpha, Myomorpha, and Hystricomorpha, but during which no one had attempted to solve the problems of the overall relationships of rodents, due to the obvious complexity of the problem. Simpson's classification (1945) was essentially an effort to retain the simplicity of the tripartite classification, even though he recognized its serious disadvantages. Subsequently, however, there has appeared a series of important papers suggesting basic modifications in rodent classification, particularly those by Lavocat (1951b, 1955 and 1956), Schaub (1953a and 1953b), Viret (*in* Grassé and Dekeyser, 1955), and Wood (1954 and 1955). Since there are several different approaches to the problem of rodent classification represented by these works, it would be well to analyze them briefly in order to explain the position that we adopt below.

If anything is clear about rodent evolution, it must be that the order has been a numerous and successful one ever since the early Eocene. Circumscribed in their evolutionary potentiality by their possession of gnawing incisors, groups of them have evolved time after time along parallel lines. Lavocat (1956) stresses this point. Parallelism, in fact, can be detected within the order as far back as the early Eocene. It is therefore always dangerous to assume that there is a special relationship between two geographically separated forms, or groups, merely because of a similarity in certain structures.[35] If the similarity amounts to practical identity, especially if the structures are slightly unusual, additional use may perhaps be made of these features as a basis for classification. But, even here, care must be used. In the study of rodent tooth patterns, for example, unworn teeth must be used wherever possible, as has been stressed by numerous authors, but there must also be a proper understanding of the significance of the structures that occur.

We do not believe that there is a touchstone for the taxonomy of rodents. No one structure (teeth, jaw muscles, angle of the jaw, bacula, or male reproductive tract) is a sure criterion for determining relationships; all available characteristics must be weighed before we can be certain that we have obtained a correct picture. Here again, Lavocat (1956) has expressed an essentially identical opinion, as has Landry (1957a) also. However, a study of living forms, representing the end stages of evolution, can never in itself give a complete picture of the relationships involved. The only way in which relationships can be demonstrated positively is by tracing the evolution of all forms through an adequate series of intermediate stages. This is far from having been accomplished as yet, which is why there are still disagreements on the classification of the order. Nevertheless, whenever a phylogeny can be established for any portion of the order, it serves as an aid in understanding the overall phylogeny; it demonstrates that some of the potential phylogenies, based on living forms, are exceedingly unlikely to have been the true ones.

Many students have expressed dissatisfaction with the neo-Brandtian classification as given by Simpson (1945), and have suggested rather extensive modifications of it, of one sort or another, a development cheerfully anticipated by Simpson himself. A few voices, however, have been raised in support of Brandt's concepts of 1855, or Tullberg's modification thereof of 1899, one of which is represented by Landry's views (1957a)

[35] Landry (1957a, pp. 33-36) discusses the importance of parallelism, remarking that it "implies that the structural similarities independently acquired in two forms are genetically related, although I have never seen this expressly stated" (Landry, 1957, p. 33). However, a number of previous authors (e.g. Haas and Simpson, 1946, p. 336; Moody, 1953, p. 107; Simpson, 1945, p. 9; 1949, pp. 181-183; Wood, 1937b, p. 175) have discussed this subject and have expressly stated that parallelism may be due to corresponding mutations of identical genes.

as to the unity of the "hystricomorphs." That we are unable to share these views should by now be evident.

Schaub has recently (1953a) presented a reclassification of the "Hystricomorpha," in which he proposes a suborder Pentalophodonta, consisting of all forms that have five-crested cheek teeth or which he believes to have been derived from ancestors having five crests. This includes two infraorders, the Palaeotrogomorpha, or Old World forms, and the Nototrogomorpha, or New World ones. His Infraorder Nototrogomorpha is the same as our Suborder Caviomorpha, the difference in taxonomic rank between the two being unimportant. But Schaub's grouping of the Nototrogomorpha and Palaeotrogomorpha into the suborder Pentalophodonta indicates his conviction, with which we cannot agree, that all pentalophate rodents are descended from the Theridomyidae. For this reason, we have continued to use Caviomorpha since it does not indicate any special relationship of Old and New World "hystricomorphs," which we feel is an important point to stress at the present stage of our knowledge. As Lavocat points out (1956), any classification, such as Schaub's, which is based on a single character or a single associated group of characters, becomes a key rather than a classification.

Viret (in Grassé and Dekeyser, 1955, pp. 1526-1564) discusses fossil rodents and their classification. In this article, he reaches what seems to be an extreme version of Schaub's classification, with three suborders: the Pentalophodonta of Schaub, the Myodonta of Schaub and an assemblage simply called Non-Pentalophodonta for the reception of the rest, namely the Sciuroidea, the Aplodontoidea (including what Wood calls the Ischyromyoidea), the Eomyoidea of Stehlin and Schaub, the Gliroidea, the Geomyoidea and the Ctenodactyloidea. We are reasonably sure that the non-pentalophodonts are not a natural group.

Kretzoi (1943) divided rodents into two suborders: the Idioglires with tritubercular teeth, including the Sciuridae, Gliridae and Paramyidae, and the Euglires with quadritubercular teeth, including all other rodents. This classification is not very useful, even from the point of view of establishing a key to the rodents.

Lavocat (1951a, pp. 72-73) divided the rodents into three divisions, Atypognathes, Hystricognathes and Sciurognathes, basically following Tullberg, but adding the Atypognathes for what Wood (1937a) included in the Ischyromyoidea. He did not elaborate on their arrangement. He stated (p. 72) that the structure of the mandible would seem to be more basic than that of the infraorbital foramen, since the latter is more subject to adaptation. But he also stated that his arrangement would tend to admit the possibility that there were numerous parallel groups independently derived from the Ischyromyoidea. On the basis of a subsequent discussion by Lavocat (1956), we feel that we are in very close agreement with him on general principles of rodent classification as well as on most of the major criteria. We do not think, however, that current evidence warrants belief that the jaw structure is any more fundamental than that of any other part of the animal. In other words, we do not see why there should not have been parallelism in the jaw structure as well as in anything else. The variable condition in the Paramyidae would have permitted either type of jaw structure to evolve one or more times. In addition, we feel that the use of the terms Hystricognathes, with two subdivisions Orthohystricognathes for the group we call Caviomorpha and Parahystricognathes for the Old World forms, implies a real relationship between the groups, which we cannot accept. In this lack of belief in a real relationship between the two (other than the derivation of both ultimately from the Paramyidae), we are supported by Lavocat himself (1951b, p. 38), although he later (1956, p. 55) suggested the possibility that the two groups were related through special Paleocene ancestors, as others have also done.

Landry (1957a) does not precisely spell out his ideas of classification above the superfamily level. He accepts, however, the three-fold division of the order into Sciuromorpha, Myomorpha and Hystricomorpha (pp. 1-2), although he feels there is more justification for subdividing the Myomorpha, at least, than the Hystricomorpha (p. 3). He believes that the shape of the angle of the jaw is a very fundamental character, separating the sciurognaths from the hystricognaths. He does not specify that these are taxonomic entities, but his work carries that implication. He follows a neo-Brandtian system, including all the hystricognaths in the Hystricomorpha, instead of separating the

Bathyergidae, as did Tullberg.[36] Landry apparently was unaware of the similarity of his views to those of Lavocat (1951a), since he makes no reference to that work. As indicated at various points above, there are a number of bases on which we disagree with his conclusions. Some are factual. Many of these have been pointed out in the text. Some rest on interpretation of the data. Primarily, however, our differences stem from different methods of approach. Landry relies to a very heavy extent on the comparative anatomy of living rodents. This is not unreasonable, since complete specimens of living rodents are available, whereas most fossil rodents are represented only by scraps. The fragmentary nature of the fossil material explains why so much paleontological work consists of discussions of tooth anatomy and the relationships it suggests. Admittedly, no study limited to the teeth can ever give a complete picture of rodent evolution, but, on the other hand, a correct phylogeny of the rodents must be in accord with the evidence of dental evolution, as well as with the evidence from other points of view. We feel very strongly that any classification, to be meaningful, must reflect the phylogeny of the forms involved. Since we disagree strongly with Landry's conclusions as to the direction of tooth evolution in the hystricomorphous rodents, we can only conclude that the other resemblances he cites, when he is correct, are the results of parallelisms between the Old and New World groups. This means either that the Hystricomorpha and Caviomorpha have a common Paleocene ancestor, distinct from the Paleocene ancestor of the other rodents (as, in fact, is postulated by Schaub, 1953a, p. 393, and by Landry, 1957a, p. 91), which we do not believe, or that the Paleocene ancestors of these forms, and of all other rodents, were paramyids, which we do believe. As pointed out above, we cannot accept the Paleocene invasion of South America by "hystricomorphs," so we fall back on the conclusion that the Hystricomorpha and Caviomorpha have derived those characters, which they hold in common, independently and subsequent to their geographic separation. This is extreme parallelism. We

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[36] A recent study of the bathyergid *Heterocephalus* emphasizes the very isolated position of this family within the order, the authors concluding that the results of their investigation indicate that the bathyergids have "myomorph" and "hystricomorph" features, but "point even more emphatically towards a complete severance of the bathyergids from all three subordinal groups of recent Rodentia" (Hill, Porter, Bloom, Seago and Southwick, 1957, p. 511).

believe it took place in the rodents. We believe, with Landry, that this means that the common ancestors of the two groups were closely related. We differ with him, however, in that we are convinced that these common ancestors must have been characterized by an assemblage of characters such that they could not have been included in either the Caviomorpha or the Hystricomorpha, and that they must have been members of the group variously called Protrogomorpha (Wood, 1937a) or Ischyromyoidea (Simpson, 1945).

Lavocat (1956, pp. 52-53) raises objections to the Suborder Sciuromorpha as used by Wood (1955), suggesting that the Sciuridae are so distinct from the ancestral stock in every respect except their tooth pattern that the ancestral stock itself should be retained as the Suborder Protrogomorpha. This we feel is a reasonable suggestion. Lavocat raises a number of other questions in regard to Wood's classification. His views seem very logical to us, whether or not we are in complete accord with the end results. Logically followed out they would result in a classification of the rodents in which only three suborders (Protrogomorpha, Myomorpha, and Caviomorpha) would contain more than three families; one suborder (Hystricomorpha) would contain three families; four suborders (Theridomorpha, Castorimorpha and perhaps two new groups, one for the Gliroidea and another for the Anomaluridae and Pedetidae) would contain two families; and three suborders (Sciuromorpha, Bathyergomorpha and a new group proposed but not named by Lavocat for the Ctenodactylidae) would contain a single family each. Under this reshuffling, or indeed under most published rearrangements of the order, the Caviomorpha, however named or ranked, becomes the largest of the major divisions of rodents, containing between 11 and 14 families, depending upon individual judgment as to whether such assemblages as the tuco-tucos and the nutrias merit familial rank. The reason is of course obvious: caviomorphs were the only group of rodents to occupy a whole continent for a very long period of time free from the competition of any other rodents. That an arrangement such as the above might best express the actual evolution of rodents is by no means impossible. It raises, however, questions concerning the classification of the order. Would it be more useful, for practical purposes and to assist in the understanding of the phylogeny, 1), to establish 11 suborders, several containing a dozen or fewer known genera; 2), to establish three suborders for the groups of considerable size (Protrogomorpha, Myomorpha and Caviomorpha), leaving all other rodents in isolated superfamilies; or, 3) to abandon suborders for the time being and use the superfamily as the unit? We think that the second of these might be the most accurate expression of current knowledge, but might prove the most confusing to the non-specialist. The last has been suggested by Simpson (*in litt.*, to Wood, dated March 22, 1954) and strongly concurred in by Ellerman (*in litt.*, to Wood, dated June 20, 1955). This would, however, in our opinion create practical difficulties in the treatment of a large and obviously natural group such as the Caviomorpha. We are in any event convinced of the utter futility of trying to continue brigading the rodents into Brandt's classical Sciuromorpha, Myomorpha and Hystricomorpha. As the early phylogeny of rodents becomes better known it may once again become possible to reduce the number of independent groups, by demonstrating relationships between two or more of the now isolated late Tertiary and Recent assemblages, possibly including ancestral forms which are now, perhaps, included in the Protrogomorpha. This time, however, has obviously not yet come.

SUMMARY

The rodents of early Oligocene Deseadan age, the earliest known from South America, are described. They are shown to represent early stages in the evolution of all the superfamilies and about half of the families of South American rodents.

The South American "Hystricomorpha" are referred to a separate suborder, the Caviomorpha, which is believed to have originated and evolved in South America.

The arrival of rodents in South America is discussed. It is concluded that they came from North America, in the latter part of the Eocene, and that, at the time of arrival, they were protrogomorphs and very probably paramyids.

It is pointed out that parallelism occurs in dental evolution of the rodents, and arguments are presented against the Stehlin-

Schaub concept of a "*Theridomys-Trechomysplan*" as the starting point for all pentalophate rodents.

The Paramyidae, as represented particularly in the early Eocene (Wasatchian) species of *Paramys*, are considered to be the most primitive known rodents, and to be either the actual or the structural ancestors of all later forms.

Comments are made on various recent proposals for the classification of the rodents, and the suggestion is made that there may be eleven or more independent groups, of subordinal rank. Forcing all rodents into the classic Sciuromorpha, Myomorpha and Hystricomorpha now seems impossible.

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